

Growth and mineral (Cs) absorption of glasswort (*Salicornia europaea* L.) cultivated in flowerpot soil watered with solar salt solution

Doo Hyun Park[†]

Department of Nano Convergence Engineering, Seokyeong University, Seoul 136-704, Korea

Received June 27, 2016/Revised July 21, 2016/Accepted August 28, 2016

Growth and mineral absorption of glasswort cultivated in flowerpot soil watered with 1, 2, and 3% solar salt solution was evaluated in relation to soil bacterial variation. Seedlings of glasswort naturally germinated in tidal mudflat were transplanted to flowerpots along with soil from the tidal mudflat field and further cultivated in the laboratory. The flowerpots were watered with 1, 2, and 3% (w/v) solar salt solution including 50 mg/L of Cs <please add what Cs full term before abbreviation i.e. cesium (Cs)> inducing pot soil to be more saline and contaminated with Cs. One, three, and seven of the 36 glassworts were cultivated in 1, 2, 3% saline soil withered <lacks meaning>. The total dry weight of glasswort grown in 1, 2, and 3% saline soil for 60 days was approximately 493, 335, and 225 g, respectively. Contents of K, Cs, Mg, Ca, and Fe accumulated in glasswort decreased but content of Na accumulated in glasswort increasing proportionally with the increase of soil salinity. Bacteria detected from the 1, 2, and 3% saline soil by temperature gradient gel electrophoresis resulted in the discovery of 30, 24, and 17 species, respectively. Thus, a soil salinity of above 1% may be an environmental factor to physiologically limit growth and mineral absorption of glasswort, therefore leading to increased variation of soil bacterial community.

Key words: Saline soil, Glasswort, Mineral absorption, Soil bacteria diversity, Cs absorption

1. Introduction

Glasswort (*Salicornia europaea*) is one of the numerous halophytes that grow in coastal areas worldwide.^{1,2)} Seawater mineral content is typically around 30-35 g/kg, except in coastal areas where streams and rivers enter the ocean.³⁾ Salinity of soil in tidal mudflat is caused by seawater (saline water) and may be irregularly varied by influences of precipitation (rain and snow) and freshwater flow from dry land.⁴⁾ The glasswort distributed on the Korean peninsula is *S. europaea* L., which grows naturally in extensive tidal mudflats and absorbs minerals originating from seawater.⁵⁾ The mineral absorption of glasswort may be a physiological function evolved to adapt to saline soil in tidal mudflat.⁶⁻⁹⁾ Thus it has been hypothesized

that if minerals contained in seawater or tidal mudflat soil are an environmental factor in the induction of glasswort to absorb minerals, glasswort may not be evolved in absorbing Cs due to its low lack of presence and low concentration in tidal mudflat soil and seawater.¹⁰⁾ If the minerals accumulated in glasswort can function as compatible solutes, balancing out internal and environmental osmotic pressure, it may be hypothesized that glasswort may absorb Cs when growing in saline soil containing Cs.¹¹⁻¹³⁾

Various soil bacteria are known to promote the growth of plants and help plants to tolerate unfavorable environments.¹⁴⁾ On the other hand, plants provide organic compounds such as root exudate and dying debris (leaves and barks) for bacteria to use as a nutrient for growth. This ecological

[†]To whom correspondence should be addressed.

symbiosis between plants and soil bacteria cannot be mutually completed without nutritional compounds produced by plants as feed for bacteria.¹⁵⁾ However, the ecological function of halophiles inhabiting the tidal mudflat has to the best of our knowledge yet to be studied or reported. Soil bacteria growing in tidal mudflat must be halophilic or halotolerant, considering that the bacteria inhabiting the tidal mudflat soils can grow in 5–20% salinity condition.^{16,17)} Halophiles that have been detected from the tidal mudflat soil are generally heterotrophs that depend upon organic compounds produced by halophytes (plants) or alternatively provided by animals.^{18,19)} Halophytes, animals, and soil bacteria inhabiting the tidal mudflat are multiply related to each other as producers, consumers, and decomposers, respectively.²⁰⁾ On the other hand, the bacterial community inhabiting the flowerpot soil may be consumer dependent upon root exudate produced by glasswort and decomposer degradation of glasswort material as the flowerpot is ecologically separated. The ecological relationship between glasswort and soil bacteria inhabiting tidal mudflat soil has not been studied but is required to be analyzed in order to evaluate the influence of soil bacteria on mineral (Cs) absorption of glasswort under controlled salinity conditions. The flowerpot that is filled with tidal mudflat soil and watered with solar salt solution (seawater) is useful as an artificial control of soil salinity.

The physiological function for Cs absorption of glasswort has yet to be studied, however, predictions can be made in its relation to mineral accumulation due to Na, K, and Cs all being common monovalent cations and belonging to the group I elements. Cs content in seawater and seashore soil is found to be a traced level (0.002 mg/Kg) that may be stably maintained, however, abundance of the radioactive isotope Cs (Cs-137) in seawater and seashore soil can be accumulated as a result of nuclear power plant accidents. Seashore soil contaminated with Cs is thought to be remediated

by using a halophyte capable of growing in saline soil thus accumulating minerals contained in seawater. Seashore soil salinity is altered by variation in environmental conditions and changes in soil salinity may influence growth and mineral accumulation of halophytes. Accordingly, glasswort is required to be cultivated in flowerpot soil to evaluate the influence of soil salinity variation on mineral (Cs) absorption of glasswort and soil bacterial variation. In this study, growth and mineral absorption of glasswort cultivated in flowerpots watered with 1, 2, 3% solar salt solution was compared and variation of soil bacterial community inhabiting flowerpot soil was analyzed.

2. Materials and Methods

2.1. Glasswort cultivation

Glasswort seedlings with roots and soil intact were collected in a tidal mudflat located on the west seashore of Anmyeon-do (Tae-an-Gun, Chungcheong-Namdo, Korea) and immediately transplanted to flowerpots on May 10, 2015. Nine glassworts were planted in each flowerpot (8,000 mL volume; 200 × 200 × 200 mm). The seedlings were cultivated under sunlight obtained through a south-facing window and were watered regularly. The glasswort pots were classified into 3 groups and 4 flowerpots for each group were prepared. Each flowerpot was regularly watered with 2,000 mL of 1, 2, and 3% solar salt solution every 2-3 days for a 60 day period based on the moisture state of the surface soil. Solar salt used for salt solution preparation was dried under sunlight without separation of leachate. The glasswort pots were watered with fresh water (0% solar salt solution) as a control test was not prepared due to glasswort being unable to grow naturally around wetland (marsh and swamp) or? in the dry land. Temperature and moisture in the laboratory were not artificially controlled. Fifty mg/L of Cs was added to the solar salt solutions used for watering. The water which was later drained from the glasswort pots after watering was

not recycled.

2.2. Soil sampling for temperature gradient gel electrophoresis (TGGE)

Approximately 2 g of soil was collected at a depth of 8–12 cm from five locations points in each glasswort pot on day 60 after transplantation. The soil collected from the five locations were mixed and placed in each pot, following this, DNA was extracted from the soil mixture using a bead beater (FastPrep-24; MP Biomedical, Solon, OH, USA) and a DNA extraction kit (Power Soil DNA isolation kit; MoBio Laboratories, Carlsbad, CA, USA). The chromosomal DNA extracted from the soil samples was used as a template to amplify 16S-rDNA.

2.3. TGGE

The 16S-rDNA amplified from the chromosomal DNA was employed as a template to amplify the 16S-rDNA V3 region. The 16S-rDNA V3 was amplified with the forward primer (eubacteria, V3 region) 341f 5'-CCTACGGGAGGCAGCAG-3' and the reverse primer (universal, V3 region) 518r 5'-ATT ACCGCGGCTGCTGG-3'. A GC clamp 5'-CGCCCG CC-GCGCGCGGCGGGCGGGCGGGGCACGGGG GGCCTACGGGAGGCAGCAG-3') was attached to the 5'-end of the GC341f primer.^{21,22)} Polymerase chain reaction (PCR) and DNA sequencing conditions were identical to those for the 16S-rDNA amplification, with the exception that a 57°C annealing temperature was used. The TGGE system (Dcode, Universal Mutation Detection System; Bio-Rad, Hercules, CA, USA) was operated in accordance with the manufacturer's recommendations. Aliquots of 60 ml of the PCR products were electrophoresed on gels containing 8% acrylamide, 8 M urea, and 20% formamide in a 1.5× TAE buffer system at a constant voltage of 100 V for 12.5 hr and then at 40 V for 0.5 hr, applying a thermal gradient of 39–52°C. Prior to electrophoresis, the gel was equilibrated to a specific temperature gradient for 30–60 min.

2.4. Amplification of DNA bands and identification

DNA was extracted from the TGGE gel and purified using a DNA gel purification kit (Accuprep; Bioneer, Daejeon, Korea). The purified DNA was amplified via the same primers and procedures used for TGGE sample preparation, to which the GC clamp was not linked to the forward primer. The species-specific identity of the amplified 16S-rDNA V3 was determined based on sequence homology in the GenBank database system.

2.5. Extraction of minerals from glasswort

Whole glasswort cultivated over a 60 day period were pulled from pots with their roots being selectively washed to remove soil particles. Water content in the whole glasswort body was determined as the difference between wet and dry weight, which was employed to determine mineral contents based on dry weight. One gram of completely dried glasswort was finely ground, immersed in 100 mL 10 mM EDTA solution, and incubated by shaking at 120 rpm and 4°C for 24 hrs to naturally extract the minerals. The glasswort slurry was centrifuged at 12,000g at 4°C for 30 minutes, and the supernatant was used for mineral analyses.

2.6. Mineral analysis

The minerals were analyzed using an inductively-coupled plasma optic emission (ICPOE) spectrometer (SPECTRO Analytical Instrument, Kleve, Germany). The dried glasswort was then ground to a size < 100 mesh. The glasswort powder was extracted with double-distilled water for 6 hrs at 4°C. The supernatant of the glasswort extract was filtered through a 0.22 mm membrane filter (Satorius, Edgewood, NY, USA) and diluted with double-distilled water. The diluted filtrate was directly injected into the ICPOE injector under specific wavelengths for Na (589.592 nm), K (766.491 nm), Cs (852.11 nm), Mg (279.553 nm), and Fe (238.204 nm). Mineral concentrations were calculated based on the absorbance obtained using standard mater-

ials (AccuTrace™ Reference Standards; AccuStandard, New Haven, CT, USA) and dilution rates.

3. Results and Discussion

3.1. Growth of glasswort in saline soil

Glasswort belongs to the halophytes that generally inhabit saline soil around tidal mudflat and salt marshes, they do not grow naturally on dry land. The reasons to why glasswort does not grow on dry land are unknown and were not studied. However, the phenomenon of biomass of glasswort grown in conditions without NaCl and with 2% NaCl was 450% and 160% lower, respectively, than that of optimal conditions with 1% NaCl.⁵⁾ On the basis of this natural attribute, previously reported data, combined with experimental data about glasswort growth taken from this study, minerals originating from seawater may be required for normal growth. Properly diluted seawater or solar salt solution (rehydrated dried seawater) may be a useful mineral source for glasswort growth. When glasswort-growing pots were watered with 1, 2, and 3% solar salt solution for 60 days, 1, 3, and 7 crops of 36 glassworts withered, respectively. Furthermore, 494, 335, and 226 g of glasswort were produced based on dry mass, respectively, as shown in Table 1. Meanwhile, the water content of glasswort did not vary significantly with differences in soil salinity. From these results it can be assumed that the optimal salinity for glasswort growth may be around 1%, with a higher salinity of 1% restricting glasswort growth in the artificially controlled soil conditions found in the flowerpot soil.^{9,23,24)} The optimal salinity for glasswort inhabiting the natural ecosystem like the tidal mudflat may be

different from that cultivated in the flowerpots on the basis of biogeochemical condition variations between mudflat and flowerpot.²⁵⁾ The major differences of biogeochemical condition between the tidal mudflat and flower pot soil are salinity and organic content. Salinity of tidal mudflat soil has to be irregularly varied by periodical submerging in seawater and the irregular inflow of freshwater dependent upon precipitation⁴⁾ in contrast to that of flowerpot soil which possessed fixed conditions of watering with solely solar salt solution. Furthermore, organic content in tidal mudflat soil is more plentiful than that in the flowerpot on the basis of biological diversity.

3.2. Influence of soil salinity on mineral (Cs) accumulation in glasswort

Ecological ability of halophytes capable of growing in saline soil may be related to the physiological function of the accumulation of minerals.²⁶⁾ The abundance of other minerals with the exception of Na decreased consistently by increasing soil salinity from 1 to 3% as shown in Table 2. Theoretically, content of minerals accumulated in the halophyte may be equivalent with or a little higher than that of the minerals contained in the pot soil for balance of osmotic pressure between plant and environment.²⁶⁾ Na is shown to be directly related to the balance of osmotic pressure due to quantities of Na accumulating in glasswort grown in 1, 2, and 3% saline soil proportionate to soil salinity. The relatively higher Na accumulated in glasswort may be a cause in limiting absorption of other minerals in order to control total mineral content.⁵⁾ Cs is not one of the general minerals accumulated in glasswort and contained in mudflat

Table 1. Yield of glasswort that was cultivated in flowerpots watered with 1, 2, or 3% solar salt solution for 60 days

Mass and content	Salinity of flowerpot soil		
	1%	2%	3%
Glasswort crops grown (withered)	35 (1)	33 (3)	29 (7)
Water content in whole glasswort (g/kg)	835.4±11.6	842.2±12.3	841.7±12.1
Mean dry mass of single glasswort (g)	14.11±0.32	10.16±0.38	7.78±0.26
Dry mass of total glassworts (g)	493.9±11.2	335.3±12.54	225.6±7.54

Table 2. Mineral content of glasswort cultivated in flowerpots watered with 1, 2, or 3% solar salt solution (SSS) for 60 days

Ionic valence	Minerals	Mineral content (mg/kg) based on fresh weight (dry weight) of glasswort		
		1% SSS	2% SSS	3% SSS
Mono valence ions	Na	10,735±349 (65,218±2,123)	12,874±401 (81,584±2,541)	14,732±458 (93,064±2,896)
	K	2,864±122 (917,380±741)	2,225±101 (14,100±640)	1,536±98 (9,703±619)
	Cs	66.15±2.27 (401.9±13.8)	51.82±2.30 (328.4±14.6)	42.17±1.95 (266.4±12.3)
Di valence ions	Mg	24.41±0.58 (148.3±3.5)	22.33±0.73 (141.5±4.6)	21.75±0.62 (137.4±3.9)
	Ca	50.78±1.42 (308.5±8.6)	45.10±0.98 (285.8±6.2)	44.28±1.17 (279.7±7.4)
	Fe	5.88±0.15 (35.7±0.9)	5.10±0.14 (32.3±0.9)	4.57±0.09 (28.9±0.6)
Mean of total content		13,742.8 (83,492.4)	15,223.2 (96,471.9)	16,380.8 (93,873.7)

*Content of Cs in the solar salt solution was 50 mg/kg.

**Iron content in flowerpot soil originated from mudflat was not previously analyzed.

soil; however, Cs added to solar salt solution for watering glasswort-growing pot soil was accumulated within the glasswort body in reverse proportion to soil salinity. Cs may not essential for glasswort growth but may function as a physiological factor for maintenance of osmotic balance on the basis of Cs being a monovalent ion, highly soluble in water, and belonging to group I elements such as Na and K. The phenomenon that glasswort accumulates Cs may be an environmental tool for the removal of Cs from the contaminated soil.²⁷⁾ Cs uptake by non-halophytes was reported to be inhibited by competition with K,²⁸⁾ however, Cs uptake by glasswort was proportional to K uptake. From these results, it is hypothesized that artificial control of Na and K content in soil contaminated with Cs may be a useful way to effectively removal Cs from contaminated soil with the use of glasswort or alternative halophytes.

3.3. Influence of soil salinity on bacterial diversity

A higher salinity of glasswort-growing pot soil than 1% resulted in the limitation of glasswort growth and biomass to be significantly reduced

(Table 1). This limitation on glasswort biomass may result in organic content in flowerpot soil to be limited as glasswort is the sole producer in the glasswort-growing pot that is ecologically separated in exception to gas exchange.²⁹⁾ Certain unaffected halophilic or halotolerant bacteria originating from the tidal mudflat soil may grow in these conditions but some may not adapt to the pot soil to which environmental and nutritional conditions differ from that of tidal mudflat soil. The TGGE bands and patterns for 16S-rDNA obtained from the glasswort-growing pot soil were characterized by differences in soil salinity and bacterial diversity (band number), both decreased significantly in proportion to soil salinity as shown in Fig. 1. Bacterial species analyzed from the glasswort-growing pot soil watered with 1, 2, and 3% solar salt solution detected 30, 24, and 17 species, respectively, as shown in Table 3.

Reduction of bacterial diversity by increasing soil salinity may not be due to salinity strength as seen by the halophiles detected from the glasswort-growing pot soil growing at higher salinity concentrations of above 5%.³⁰⁾ This clear decreasing tendency of bacterial diversity by a difference of 1% salinity

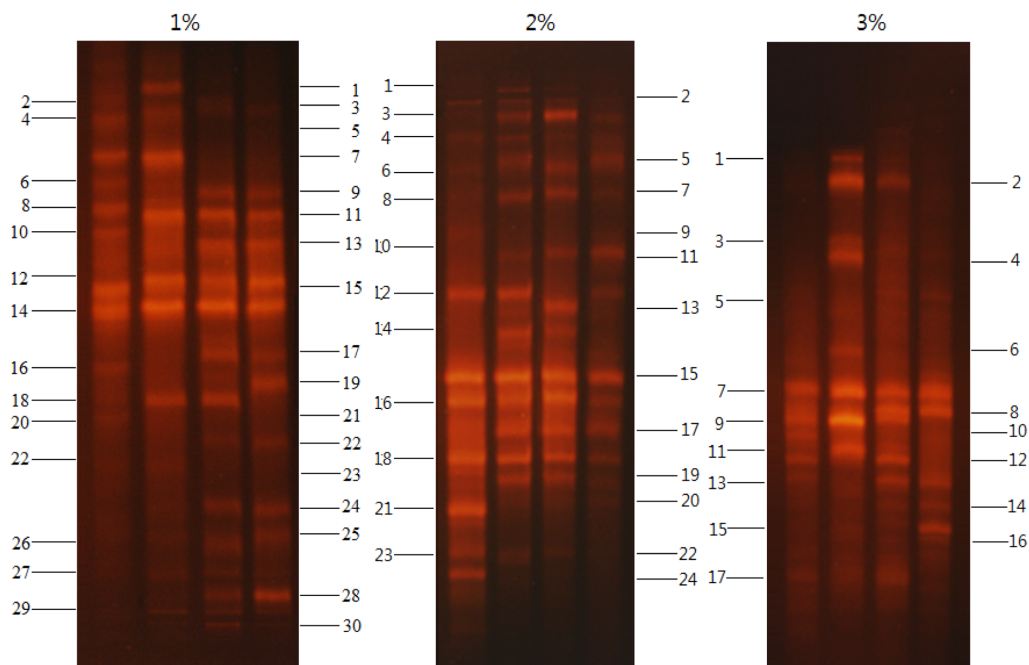


Fig. 1. A TGGE profile for the 16S-rDNA variable region (bases 341-518) that was amplified with chromosomal DNA extracted from glasswort-cultivating pot soil watered with 1, 2, and 3% solar salt solution.

may not be related to salinity but rather to the nutritional conditions of flowerpot soil as all halophiles detected from the flowerpot soil were heterotrophs.³¹⁾

Nutritional sources for halophiles inhabiting tidal mudflat soil are widely varied in plants and animals that are ecologically balanced but those halophiles grown in flowerpots there may be limitations on the exudation of decaying organic debris of the glasswort.³²⁾ Accordingly, diversity of halophiles inhabiting the glasswort-growing pots may be determined by the glasswort growth state (Table 1). Certain soil bacteria that depend nutritionally upon plants form a symbiotic relationship with the plants by producing growth factors, activating mineral absorption, solubilizing phosphate, and resisting abiotic environmental stressors.³³⁻³⁵⁾ The bacteria inhabiting the glasswort-growing pot soil may be evaluated positively to help glasswort on the basis of the results that approximate 97, 92, and 81% of glassworts survived and grew in the flowerpots watered

with 1, 2, and 3% solar salt solution, respectively. However, the ecological relationship between glasswort and soil bacteria may be limited in the flowerpots watered with 2 and 3% solar salt solution as seen by a decrease in the producers' biomass. Accordingly, optimal environmental condition for general growth of producers (plants) is required to be optimized for maintenance of the ecological relationship between plants and soil bacteria.

4. Conclusion

Glasswort is one of the most general halophytes inhabiting naturally found tidal mudflat located in the west and southern seashores of South Korea accumulating various minerals contained in seawater. However, the optimal salinity for glasswort growth was 1% which is significantly lower than seawater salinity (3-3.5%). Na may be a functional factor in controlling the osmotic balance between glasswort and soil hypothesized by the accumula-

Table 3. Bacterial species detected from glasswort-cultivating pots that were watered with 1, 2, and 3% solar salt solution, respectively, for 60 days

TGGE Band No	1% salinity	2% salinity	3% salinity
1	<i>Sulfurimonas autotrophica</i>	<i>Sulfurospirillum halorespirans</i>	<i>Halomonas almeriensis</i>
2	<i>Sulfurospirillum halorespirans</i>	<i>Alcanivorax borkumensis</i>	<i>Bowmanella denitrificans</i>
3	<i>Halomonas almeriensis</i>	<i>Sulfurimonas autotrophica</i>	<i>Halomonas koreensis</i>
4	<i>Arcobacter halophilus</i>	<i>Arcobacter halophilus</i>	<i>Halomonas janggokensis</i>
5	<i>Sulfurospirillum deleyianum</i>	<i>Sulfurospirillum deleyianum</i>	<i>Marinobacter santoriniensis</i>
6	<i>Sulfurimonas denitrificans</i>	<i>Sulfurimonas denitrificans</i>	<i>Marinobacterium nitratireducens</i>
7	<i>Marinobacterium sediminicola</i>	<i>Marinobacterium sediminicola</i>	<i>Alishewanella aestuarii</i>
8	<i>Marinimicrobium agarilyticum</i>	<i>Marinimicrobium agarilyticum</i>	<i>Oceanisphaera donghaensis</i>
9	<i>Marinimonas posidonica</i>	<i>Marinimonas posidonica</i>	<i>Sulfuricurvum kujiense</i>
10	<i>Rheinheimera perlucida</i>	<i>Rheinheimera perlucida</i>	<i>Rheinheimera aquimaris</i>
11	<i>Bowmanella denitrificans</i>	<i>Sulfurospirillum barnesii</i>	<i>Marinobacterium sediminicola</i>
12	<i>Sulfurospirillum barnesii</i>	<i>Glaciecola lipolytica</i>	<i>Halomonas halmophila</i>
13	<i>Halomonas koreensis</i>	<i>Halovibrio denitrificans</i>	<i>Halomonas halophila</i>
14	<i>Glaciecola lipolytica</i>	<i>Thiohalorhabdus denitrificans</i>	<i>Reinekea blandensis</i>
15	<i>Halovibrio denitrificans</i>	<i>Oceanisphaera donghaensis</i>	<i>Marinobacterium stanieri</i>
16	<i>Thiohalorhabdus denitrificans</i>	<i>Sulfuricurvum kujiense</i>	<i>Alkalimonas delamerensis</i>
17	<i>Alishewanella aestuarii</i>	<i>Rheinheimera aquimaris</i>	<i>Hahella chejuensis</i>
18	<i>Oceanisphaera donghaensis</i>	<i>Halomonas halophila</i>	
19	<i>Sulfuricurvum kujiense</i>	<i>Alcanivorax venustensis</i>	
20	<i>Rheinheimera aquimaris</i>	<i>Oceanimonas smirmovii</i>	
21	<i>Oceanimonas smirmovii</i>	<i>Halotalea alkalilenta</i>	
22	<i>Alcanivorax venustensis</i>	<i>Aestuariibacter salexigens</i>	
23	<i>Halomonas halmophila</i>	<i>Simiduia agarivorans</i>	
24	<i>Halomonas halophila</i>	<i>Reinekea blandensis</i>	
25	<i>Aestuariibacter salexigens</i>		
26	<i>Simiduia agarivorans</i>		
27	<i>Reinekea blandensis</i>		
28	<i>Marinobacterium stanieri</i>		
29	<i>Alkalimonas delamerensis</i>		
30	<i>Halotalea alkalilenta</i>		

tion of Na in glasswort cultivated in flowerpot soil, increasing proportionally while other minerals decreased proportionally to soil salinity. Furthermore, Cs accumulated in glasswort also decreased proportionally to the soil salinity of K. This experimental data clearly depicts glasswort growth and mineral accumulation of glasswort being related to the soil salinity and may be useful for bioremediation of contaminated soil with Cs. Cs absorption of glasswort may be controlled by various adjustments of Na and K content in soil. Conclusively, both biomass and Cs uptake of glasswort is required to be optimized by the separate control of Na,

K, and Cs content in soil with the evaluation of the relationship between glasswort growth, bacterial diversity, and organic content in soil.

References

1. A.J. Brereton, "The structure of the species populations in the initial stages of salt-marsh succession", *Journal of Ecology*, **1971**, 59, 321-338.
2. I. A. Ungar, D. K. Benner, and D. C. McGraw, "The distribution and growth of *Salicornia europaea* on an inland salt pan", *Ecology*, **1979**, 60, 329-336.
3. R. Pawlowicz, "Key physical variables in the ocean: temperature, salinity and density", *Nature Education*

- Knowledge*, **2013**, 4, 13.
4. P. Adam, "Salt Marsh Ecology", **1990**, 1-71, Cambridge University Press, Cambridge, England.
 5. S. A. Ushakova, N. P. Kovaleva, I. V. Grinbovskaya, V. A. Dolgushev, and N. A. Tikhomirova, "Effect of NaCl concentration on productivity and mineral composition of *Salicornia europaea* as a potential crop for utilization NaCl in LSS", *Advances in Space Research*, **2005**, 36, 1349-1353.
 6. T. J. Flowers and T. D. Colmer, "Salinity tolerance in halophytes", *New Phytologist*, **2008**, 179, 945-963.
 7. C. D. Foy, "Soil chemical factors limiting plant root growth", *Advances in Soil Science*, **1992**, 19, 97-149.
 8. B. Gul, R. Ansari, and M. A. Khan, "Salt tolerance of *Salicornia utahensis* from the great basin desert", *Pakistan Journal of Botany*, **2009**, 41, 2925-2932.
 9. M. A. Khan, B. Gul, and D. J. Weber, "Effect of salinity on the growth and ion content of *Salicornia rubra*", *Communication in Soil Science and Plant Analysis*, **2001**, 32, 2965-2977.
 10. E. P. Glenn, J. J. Brown, and E. Blumwald, "Salt tolerance and crop potential of halophytes", *Critical Review in Plant Science*, **1999**, 18, 227-255.
 11. T. J. Flowers, P. F. Troke, and A. R. Yeo, "The mechanism of salt tolerance in halophytes", *Annual Review of Plant Physiology*, **1977**, 28, 89-121.
 12. S. Lv, P. Jiang, X. Chen, P. Fan, X. Wang, and Y. Li, "Multiple compartmentalization of sodium conferred salt tolerance in *Salicornia europaea*", *Plant Physiology and Biochemistry*, **2012**, 51, 47-52.
 13. Q. Zheng, L. Liu, Z. Liu, J. Chen, and G. Zhao, "Comparison of the response of ion distribution in the tissues and cells of the succulent plants *Aloe vera* and *Salicornia europaea* to saline stress", *Journal of Plant Nutrition and Soil Science*, **2009**, 172, 875-883.
 14. S. Timmusk and G. H. Wagner, "The plant-growth promoting rhizobacterium *Pacenibacillus polymyxa* induces changes in biotic and abiotic stress responses", *Molecular Plant Microbe Interaction*, **1999**, 12, 951-959.
 15. S. D. Siciliano and J. J. Germida, "Mechanisms of phytoremediation: biochemical and ecological interactions between plants and bacteria", *Environmental Review*, **1998**, 6, 65-79.
 16. F. Rodríguez-Valera, F. Ruiz-Berraquero, and A. Ramos-Cormenzana, "Isolation of extreme halophiles from seawater", *Applied and Environmental Microbiology*, **1979**, 38, 164-165.
 17. M. J. Aileen, R. T. Lancer, R. Z. Sam, and T. G. Eric, "Partial characterization of two moderately halophilic bacteria from a Kansas salt marsh", *Prairie Naturalist*, **2007**, 39, 29-39.
 18. P. A. W. de Wilde and B. R. Kuipers, "A large indoor tidal mud-flat ecosystem", *Helgoländer Wissenschaftliche Meeresuntersuchungen*, **1977**, 30, 334-342.
 19. B. L. Welsh, "Compartive nutrient dynamics of a marsh-mudflat ecosystem", *Estuarine and Coastal Marine Science*, **1980**, 10, 143-164.
 20. B. R. Kuipers, P. A. W. de Wilde, and F. Creutzberg, "Energy flow in a tidal flat ecosystem", *Marine Ecology Progress Series*, **1981**, 5, 215-221.
 21. C. A. Eichner, R. W. Erb, K. N. Timmis, and I. Wagner-Döbler, "Thermal gradient gel electrophoresis analysis of bioprotection from pollutant shocks in the activated sludge microbial community", *Applied and Environmental Microbiology*, **1999**, 65, 102-109.
 22. P. Y. Cheung and B. K. Kinkle, "Mycobacterium diversity and pyrene mineralization in petroleum-contaminated soils", *Applied and Environmental Microbiology*, **2001**, 67, 2222-2229.
 23. B. Amiri, M.H. Assareh, M. Jafari, B. Rasuoli, H. Arzani, and A.A. Jafari, "Effect of salinity on growth, ion content and water status of glasswort (*Salicornia herbacea* L.)", *Caspian Journal of Environmental Science*, **2010**, 8, 79-87.
 24. D. Katsching, R. Broekman, and J. Rozema, "Salt tolerance in the halophyte *Salicornia dolichostachya* moss: growth, morphology, and physiology", *Environmental and Experimental Botany*, **2013**, 92, 32-42.
 25. G. F. Blanchard, J. M. Guraini, F. Orvain, and P. G. Sauriau, "Dynamic behavior of benthic microalgal biomass in intertidal mudflats", *Journal of Experimental Marine Biology and Ecology*, **2001**, 264: 85-100.
 26. E. P. Glenn and J. W. O'Leary, "Relationship between salt accumulation and water content of dictyledonous halophytes", *Plant Cell & Environment*, **1984**, 7, 253-261.
 27. N. A. Tikhomirova, S. A. Ushakova, N. P. Kovaleva, I. V. Gribovskaya, and A. A. Tikhomirov, "Influence of high concentration of mineral salts on production process and NaCl accumulation by *Salicornia europaea* plants as a constituent of the LSS phototroph link", *Advances in Space Research*, **2005**, 35, 1589-1593.
 28. G. Shaw and J. N. B. Bell, "Competitive effect of potassium and ammonium on caesium uptake kinetics in wheat", *Journal of Environmental Radioactivity*, **1991**, 13, 283-296.
 29. C. Bertin, X. Yang, and L. A. Weston, "The role of root exudates and allelochemicals in the rhizosphere", *Plant and Soil*, **2003**, 256, 67-83.
 30. A. Ventosa, J. J. Nieto, and A. Oren, "Biology of mod-

- erately halophilic aerobic bacteria”, *Microbiology and Molecular Biology Review*, **1998**, 62, 504-544.
31. M. A. Cunha, R. Pedro, M. A. Almeida, and M. H. Silva, “Activity and growth efficiency of heterotrophic bacteria in a salt marsh (Ria de Aveiro, Portugal)”, *Microbiological Research*, **2005**, 160, 279-290.
 32. H. P. Bais, T. L. Weir, L. G. Perry, S. Gilroy, and J. M. Vivanco, “The role of root exudates in rhizosphere interactions with plants and other organisms”, *Annual Review of Plant Biology*, **2006**, 57, 233-266.
 33. F. Ahmad, I. Ahmad, and M. S. Khan, “Screening of free-living rhizospheric bacteria for their multiple plant growth promoting activities”, *Microbiological Research*, **2008**, 163, 173-181.
 34. P. A. H. M. Bakker, R. F. Doormbos, C. Zamioudis, R. L. Berendsen, and C. M. Pieterse, “Induced systemic resistance and the rhizosphere microbiome”, *Plant Pathology Journal*, **2013**, 29, 136-143.
 35. H. Rodríguez and R. Fraga, “Phosphate solubilizing bacteria and their role in plant growth promotion”, *Biotechnology Advances*, **1999**, 17, 319-339.