Solute patterns of four halophytic plant species at Suncheon Bay in Korea

Sung-Chul Choi[1], Deok-Gyun Choi[1], Jeong-Sook Hwang[1], Jong-Guk Kim[2] and Yeon-Sik Choo[1,*]

[1]Department of Biology, Kyungpook National University, Daegu 702-701, Korea
[2]Department of Life Science and Biotechnology, Kyungpook National University, Daegu 702-701, Korea

Abstract

To investigate the solute pattern of salt marsh plants in Suncheon Bay in Korea, plants and soil samples were collected at three sites from July to September 2011. The soil pH around the investigated species was weakly alkaline, 6.9–8.1. The total ion and Cl^- content of site 1 gradually increased, while those of site 2 and site 3 were lowest in August and highest in September. The exchangeable Ca^{2+}, Mg^{2+} and K^+ in the soil were relatively constant during the study period, but the soil exchangeable Na^+ content was variable. *Carex scabrifolia* and *Phragmites communis* had constant leaf water content and very high concentrations of soluble carbohydrates during the study period. However, *Suaeda malacosperma* and *S. japonica* had high leaf water content and constant very low soluble carbohydrate concentrations. *Carex scabrifolia* accumulated similar amounts of Na^+ and K^+ ions in its leaves. *Phragmites communis* contained a high concentration of K^+ ions. *Suada japonica* and *S. malacosperma* had more Na^+ and Cl^- ions than K^+ ions in their leaves. *Suaeda japonica* had higher levels of glycine betaine in its leaves under saline conditions than *C. scabrifolia* and *P. communis*. Consequently, the physiological characteristics of salt marsh chenopodiaceous plants (*S. japonica* and *S. malacosperma*) were the high storage capacity for inorganic ions (especially alkali cations and chloride) and accumulation of glycine betaine, but monocotyledonous plant species (*C. scabrifolia* and *P. communis*) showed high K^+ concentrations, efficient regulation of ionic uptake, and accumulation of soluble carbohydrates. These characteristics might enable salt marsh plants to grow in saline habitats.

Key words: halophyte, inorganic solutes, organic solutes, salt marsh

INTRODUCTION

Salinity can cause two distinct types of stress in plants, making it a major limiting factor for agricultural production. Salt stress in the soil generally involves osmotic stress, caused by the greater difficulty of water absorption, and ionic stress, associated with the effects of sodium ions on diverse cellular functions, decreasing nutrient absorption, enzyme activities, photosynthesis, and metabolism (Zhu 2001, Munns 2002). Thus, plants in saline soil must cope with physiological drought and ion toxicity, and also need to maintain intracellular ion balance and regulate pH outside the roots.

Salt marshes have often been considered to be wastelands. However, they are habitats for many halophytes with high economic and medicinal importance (Khan et al. 2000, Parida and Das 2005). It is necessary for plants growing well under saline conditions to have a greater

salt tolerance, and this characteristic has influenced the ecological distribution of various plants (Flowers and Colmer 2008). By accumulating inorganic ions, halophytes absorb water by maintaining a high osmotic potential. Glycine betaine and proline are compatible solutes that accumulate in response to osmotic stress, and the accumulation of these osmolytes represents an important adaptive response to salt and drought stress (Di Martino et al. 2003, Moghaieb et al. 2004). It is essential to study plants with resistances to various saline environments in order to develop crops that can withstand increased salinity (Chinnusamy et al. 2005).

Increased salinization of arable land and decline of fresh water supplies have developed new interest in plant materials possessing salt tolerance, such as halophytes (Koyro et al. 2013). Halophytes are being used not only as food crops and fodder, but also as ground cover to protect against soil erosion. Through the root development, soil porosity increases, and the physical condition of the soil is subsequently improved over time (Rozema and Flowers 2008).

Suaeda japonica, S. malacosperma, Phargmites communis and *Carex scabrifolia* are the main species distributed on saline marsh habitats in Suncheon Bay in Korea. Most studies on salt marshes have focused on the environmental factors affecting vegetation characteristics and the distribution of halophytes (Kim et al. 1986, Lee 1988, Min and Kim 1999, Yang 1999, Kefu et al. 2002, Lee et al. 2003, Choi et al. 2004, Choi et al. 2012). However, their adaptive mechanisms under dry and saline conditions have not yet been clearly described.

The aim of this research was to study the organic and inorganic solute levels in salt marsh plants due to seasonal changes.

MATERIALS AND METHODS

Study site

The study site is located in Suncheon Bay Ecological Park, Korea (N 34°52′17.1″, E 127°30′11.9″; Tokyo datum). The annual mean temperature and precipitation in the study area were 13.9°C and 1308 mm, respectively. This study site is a salt marsh where communities of *Phragmites communis* are predominate (Fig. 1).
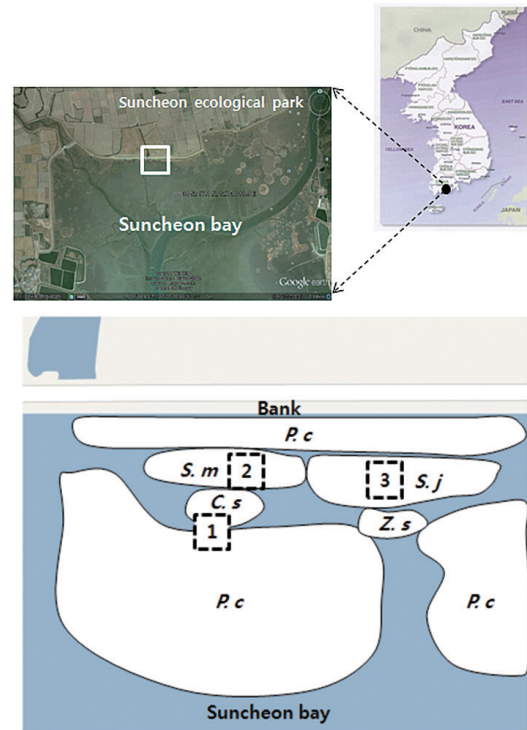
Fig. 1. A map showing the study site, Suncheon Bay Ecological Park, in Korea (N 34°52′17.1″, E 127°30′11.9″; Tokyo datum). Numbers indicate the soil sampling sites (site 1, *Phragmites communis* and *Carex scabrifolia* community; site 2, *Suaeda malacosperma*; site 3, *Suaeda japonica*). *P.c, Phragmites communis*; *C.s, Carex scabrifolia*; *S.m, Suaeda malacosperma*; *S.j, Suaeda japonica*; *Z.s, Zoysia sinica*.

Soil sampling and measurement of chemical characteristics

Soil samples from 15–20 cm below the soil surface around the plant were collected to analyze the chemical characteristics of rhizospheric soil. The collected soil samples were air dried. Soil samples (5 g) were added to distilled water (25 mL) and were shaken for 1 h. The soil solution was then filtered through filter paper (Whatman No. 40, 110 mm; Whatman, Little Chalfont, England). Soil pH, total ionic contents (calculated as NaCl equivalents), and chloride contents were measured by using a pH meter (Orion US/710; Thermo Orion, Beverly, MA, USA), electronic conductivity meter (Mettler Check Mate 90; Mettler Toledo Inc., Columbus, OH, USA), and chloride titrator (Titrators DL 50; Mettler Toledo Inc.), respectively.

Exchangeable cations (Na^+, K^+, Ca^{2+}, Mg^{2+}) in soil solution were extracted by 1 N ammonium acetate (CH_3COONH_4) and quantified by using inductively coupled plasma atomic emission spectroscopy (ICP-AES) (Optima 7300 DV; Perkin Elmer, Waltham, MA, USA).

Plant sampling and plant water content

Carex scabrifolia Steud., *P. communis* Trin., *S. japonica* Makino, and *S. malacosperma* Hara were sampled on July 29, August 22, and September 28, 2011. After the direct determination of fresh weight in their habitats, leaf samples were dried in an oven at 70°C for 3 days to determine dry weight. Plant water (pw) content was measured as the difference between the fresh weight and dry weight.

Measurement of inorganic ions

The dried plant material was ground to a homogeneous powder and extracted with 95°C distilled water for 1 h, after which the sample was filtered with a GF/A filter (Whatman, 4.7 cm). Inorganic cations (Na^+, K^+, Ca^{2+} and Mg^{2+}) were determined by ICP-AES (Optima 7300 DV; Perkin Elmer). The chloride content was measured using a chloride titrator (Titrators DL 50; Mettler Toledo Inc.).

Measurement of water-soluble carbohydrates, osmolality and amino acids

Total soluble carbohydrates of the plants were assayed using the phenol-sulfuric acid method (Chaplin and Kennedy 1994). Plant extract (20 μL) was mixed with 580 μL of distilled water, 400 μL of 5% phenol, and 400 μL of sulfuric acid, and the solution was allowed to stand for 10 min before being shaken vigorously. Total carbohydrates were quantified by determining the absorbance at 490 nm by using a UV mini 1240 spectrophotometer (Shimadzu, Kyoto, Japan) after 30 more minutes. Glucose (2–40 μg in 200 μL) was used as a standard solution.

Osmolality was measured by cryoscopy using a Micro-Osmometer 3MO osmometer (Advanced Instruments, Needham Heights, MA, USA).

Free amino acids were quantified using an L-8900 amino acid analyzer (Hitachi, Tokyo, Japan).

Measurement of glycine betaine

The extract was diluted with 2 N H_2SO_4 (1:1 v/v) and 0.5 mL of the acidified extract was cooled in ice water for 1 h. Later, 0.2 mL of cold potassium tri-iodide solution was added and mixed by vortex, and the tubes were stored at 4°C for 15 min and centrifuged at 10,000 rpm for 15 min. The supernatant was aspirated with a fine-tipped glass tube. The periodide crystals were dissolved in 9 mL of 1,2-dichloroethane with vigorous shaking. After 2.5 h, the absorbance was determined at 365 nm in a spectropho-
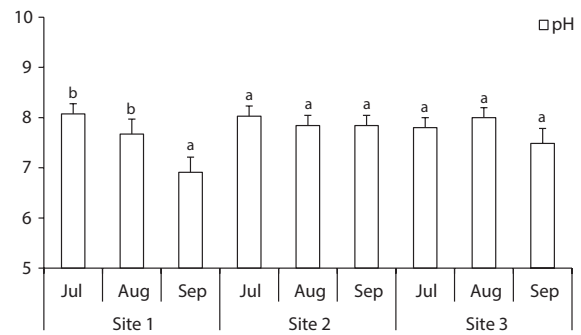
Fig. 2. Changes in the soil pH of *Carex scabrifolia*, *Phragmites communis*, *Suaeda malacosperma*, and *S. japonica*. Soil samples were collected between July and September, 2011. Different letters indicate significant differences among three months from Duncan's test for responses at sites separately ($P < 0.05$, $N = 3$).

tometer. Glycine betaine (200 μg in 1 N H_2SO_4 1000 mL) was used as a standard solution.

Statistical analyses

Data were analyzed by analysis of variance (ANOVA) using SPSS ver. 19.0 (SPSS Inc., Chicago, IL, USA). Graphs show means with standard deviation (SD). A Duncan's multiple range test was carried out to determine significant differences ($P < 0.05$, $N = 3$) among the groups.

RESULTS AND DISCUSSION

Chemical characteristics of soil

The soil was sampled at three sites (*Carex scabrifolia* and *Phragmites communis* from site 1; *Suaeda malacosperma* from site 2; *S. japonica* from site 3) once a month from July to September in 2011. The habitats of the investigated plant species were weakly alkaline, with a pH between 6.9 and 8.1. Soil samples from site 1 (*C. scabrifolia* and *P. communis*) and site 3 (*S. japonica*) showed significant changes in pH, while site 2 (*S. malacosperma*) remained relatively constant during the study period. Soil pH was generally high in July and low in September (Fig. 2).

The total ion and Cl⁻ contents in soil of site 1 gradually increased, while they were low at site 2 and site 3 in August and high in September. The soil of site 2 (*S. malacosperma*) had a low total ion content of 133.7 μmol/g soil in August.

The exchangeable Ca^{2+}, Mg^{2+} and K^+ contents of the soil were relatively constant during the study period, but the
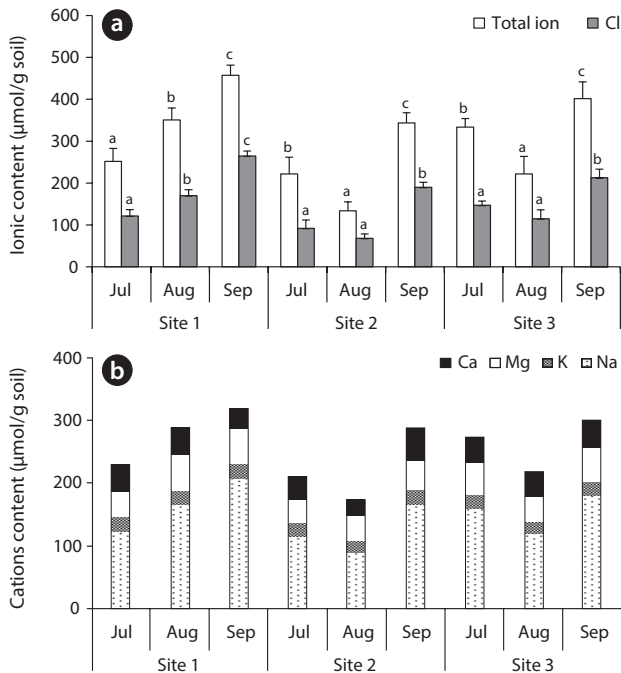
Fig. 3. Changes of (a) total ions and chloride contents and (b) exchangeable cation contents (μmol/g soil) in soil of *Carex scabrifolia*, *Phragmites communis*, *Suaeda malacosperma*, and *S. japonica*. Soil samples were collected between July and September in 2011. The different letters in (a) indicate significant differences among three months from Duncan's test for the response of the total ions and chloride separately ($P < 0.05$, $N = 3$).
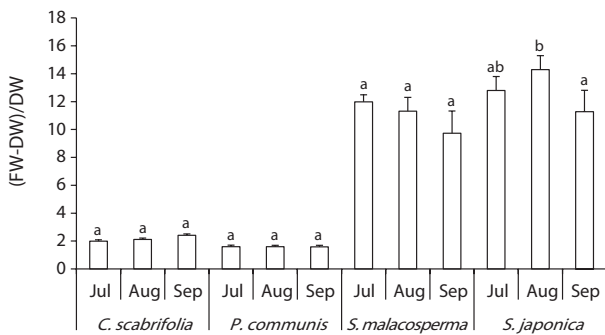
Fig. 4. Changes in the ratio of water contents to dry weight in leaves of *Carex scabrifolia*, *Phragmites communis*, *Suaeda malacosperma*, and *S. japonica* between July and September in 2011. The different letters indicate significant differences from Duncan's test for the response of species separately ($P < 0.05$, $N = 3$).

exchangeable Na^+ content was variable, showing a similar pattern to the Cl^- content (Fig. 3). Saline land of Korea's west coast has an Na^+ concentration of 160–200 μmol/g soil (Choo et al. 1999), which was relatively close to the ion content of site 1 (*C. scabrifolia* and *P. communis*) and site 3 (*S. japonica*) within the investigation area. The regions where *S. malacosperma* was found had lower Na^+ contents than site 1 and site 3.

## Plant physiological characteristics

The ratio of water content to dry weight in leaves is described in Fig. 4. The ratio of water content to dry weight in *C. scabrifolia* and *P. communis* ranged 2.0–2.4 and 1.6–1.7, respectively. Both plants had constant water content in their leaves during the entire study period. However, the leaf water content of *S. malacosperma* (9.7–12.0) and *S. japonica* (11.3–14.3), belonging to Chenopodiaceae, decreased after August. Succulence is a typical morphological adaptation to osmotic stress and is contributed to salt regulation by increasing the vacuolar volume available for ion accumulation (Khan et al. 2000, Qi et al. 2009). *Suaeda japonica* and *S. malacosperma* maintained a high ratio of water and tissue succulence to avoid ion toxicity by increasing storage area and diluting accumulated Na^+ and Cl^-.

All of the investigated species tended to accumulate soluble carbohydrates in their leaves, but the contents differed among the plant species (Fig. 5). *Carex scabrifolia* and *P. communis* had very high concentrations of soluble carbohydrates. The soluble carbohydrate contents of both plants were low in July and increased rapidly in September. *Suaeda malacosperma* and *S. japonica* had very low but constant soluble carbohydrate concentrations in their leaves; however, soluble carbohydrate concentration increased in September due to the decreased water contents in their leaves. Monocotyledonous families accumulate more soluble carbohydrates than dicotyledonous families in order to maintain a sufficiently low osmotic potential in saline habitats (Choo and Albert 1997, 1999).

The osmolality of *C. scabrifolia* and *P. communis* leaves slightly increased during the study period, but *S. japonica* and *S. malacosperma* showed a distinct increase in September. The osmolality was highest in September in all of the plant species (Fig. 6a). The total ion content of *C. scabrifolia* remained constant while *P. communis* slightly decreased, and that of *S. japonica* and *S. malacosperma* increased in September (Fig. 6a). According to the ecophysiological characteristics of each plant species, the cation patterns of the four investigated plant species remained constant throughout the study period. *Carex scabrifolia* accumulated similar concentrations of both Na^+ and K^+ ion in the leaves and showed efficient regulation of ionic uptake. The genus *Carex* and some other representatives of Cyperaceae, for example, could regulate their mineral metabolism especially well, being excluders in ion-rich and accumulators in ion-poor habitats. A balanced uptake of ions was accomplished by an efficient
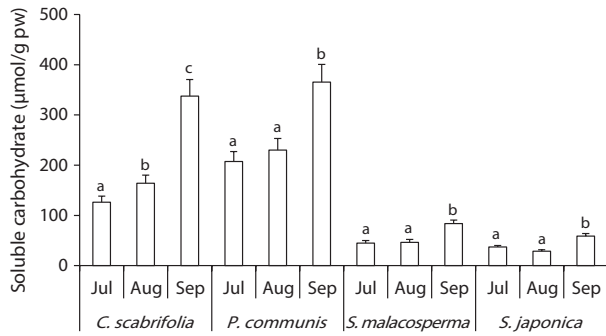
Fig. 5. Changes in soluble carbohydrate content in leaves of *Carex scabrifolia*, *Phragmites communis*, *Suaeda malacosperma*, and *S. japonica* between July and September in 2011. The different letters indicate significant differences from Duncan's test for the response of species separately ($P < 0.05$, $N = 3$); pw, plant water content.
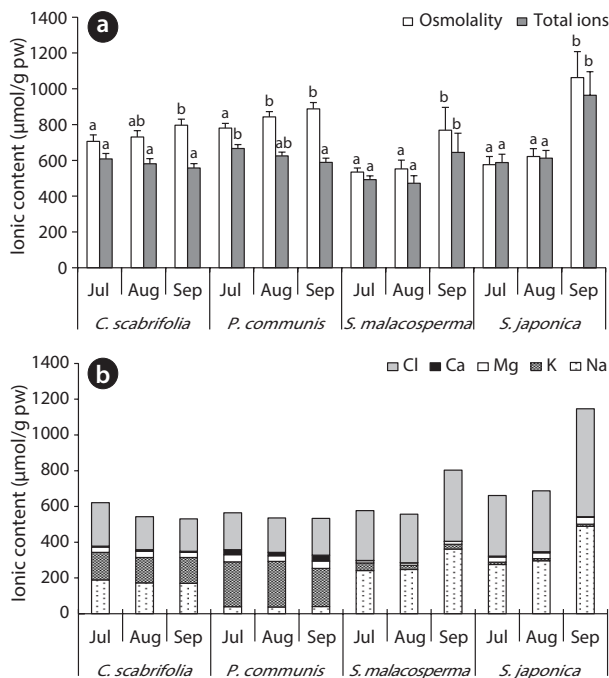
Fig. 6. Changes of (a) osmolality and total ion contents and (b) chloride and cation contents in leaves of *Carex scabrifolia*, *Phragmites communis*, *Suaeda malacosperma*, and *S. japonica* between July and September in 2011. The different letters indicate significant differences from Duncan's test for the response of total ions and chloride separately ($P < 0.05$, $N = 3$); pw, plant water content.

regulation metabolism that also prevented the uptake of potentially toxic amounts of ions (Choo and Albert 1997, 1999). *Phragmites communis* contained a high concentration of K^+ ions despite the low exchangeable K^+ in the soil. *Suaeda japonica* and *S. malacosperma* accumulated significantly higher amounts of Na^+ and Cl^- than K^+ in their leaves and had a small amount of soluble Ca^{2+} ions in their leaves (Fig. 6b). Deleterious effects of salinity are thought

to result from low water potentials, ion toxicities, nutrient deficiencies, or a combination of these factors. Na^+ in high concentrations in the soil reduces the amounts of available K^+, Mg^{2+}, and Ca^{2+}; this is also the case when Na^+ displaces membrane-bound Ca^{2+}. In addition, Na^+ may have a direct toxic effect, such as when it interferes with the function of potassium as a cofactor in various reactions (Cramer et al. 1985, Khan et al. 2000). Salt tolerance is often seen as the interaction of absorption, transport, and excretion processes, which allows for effective osmotic adjustment by means of salt accumulation. For members of the Chenopodiaceae (such as *Suaeda japonica* and *S. malacosperma*), the ability to withstand high external salt concentrations appears to depend on osmotic adjustment, most commonly with Na^+ and Cl^-, but, because these elements are toxic, their concentrations in the cytoplasm are maintained at substantially lower levels than in the vacuoles.

The content of free amino acids in the leaves of *S. malacosperma* and *S. japonica* was found to be very low and contained a small amount of proline. *Phargmites communis* accumulated higher levels of free amino acids in its leaves under saline conditions than the chenopodiaceous plants, and contained more amino acids, such as arginine, lysine, histidine, glycine, serine, and proline (Table 1).

Plants stressed by low water potential are known to accumulate amino acids such as arginine, lysine, histidine, glycine, and serine, as well as amide compounds such as glutamine and asparagine (Flores and Galston 1984,

Table 1. Free amino acid content (µmol/g plant water) in leaves of four halophytic plant species in the study sites in August 2011

	C. scabrifolia	P. communis	S. malacosperma	S. japonica
Asp	2.0	9.2	0.8	0.5
Thr	2.5	5.0	0.7	0.6
Ser	2.0	5.6	0.6	0.5
Glu	1.4	3.8	2.5	1.5
Gly	1.6	2.9	0.6	0.4
Ala	3.0	11.7	1.4	0.8
Cys	1.9	0.0	0.5	0.4
Val	4.6	11.6	1.7	1.2
Met	0.0	0.0	0.3	0.6
Ile	2.6	4.8	0.9	0.6
Leu	5.1	14.1	1.7	1.4
Tyr	3.6	8.2	2.4	1.1
Phe	2.7	5.8	2.6	1.6
Lys	2.0	3.0	1.7	0.8
His	0.8	1.4	0.4	0.2
Arg	1.2	2.0	0.7	0.5
Pro	2.9	8.2	0.9	1.1
Total	58.0	124.6	27.2	21.23

Pulich 1986, Hartzendorf and Rolletschek 2001). The accumulation of proline, a compatible solute, is a common metabolic response of higher plants to water deficits, salinity stress, and cold stress, and proline accumulation may play a major role in osmotic adjustment. As proline was shown to minimize cellular damage by enhancing the stability of proteins and membranes, proline content was shown to increase when a plant was subjected to salt stress. Proline is slowly accumulated until a plant reaches a critical salinity level. Exceeding this salt concentration, a greater reaction occurs and proline is accumulated in very high amounts (Voetberg and Sharp 1991, Rhodes and Hanson 1993). Based on the low content of proline in the investigated *Suaeda malacosperma* and *S. japonica*, proline did not seem to contribute to the osmotic regulation of this plant. However, *C. scabrifolia* and *P. communis* accumulated higher levels of proline in their leaves under salt conditions than the chenopodiaceous plant species.

The content of glycine betaine in the leaves of *P. communis* was very low. *Suaeda japonica* accumulated higher levels of glycine betaine in their leaves under saline conditions than *C. scabrifolia* and *P. communis* (Table 2). The osmotic potential in leaves decreases under saline conditions due to the accumulation of salt and increasing levels of glycine betaine, which represents an important adaptive response to osmotic stress. Thus, these plants maintain a low osmotic potential, which is important for the absorption of water under low soil water potential. Generally, chenopodiaceous plant species are known to accumulate glycine betaine for osmoregulation (McCue and Hanson 1990). If salt is taken up by a plant and accumulates in the cytoplasm of cells, it can lead to toxicity. For plants to maintain their ability to take up water and prevent dehydration, as well as positive functions in relation to the maintenance of membrane integrity and the stability of other cellular structures, their osmotic potential needs to be lower than that in the soil. In principle, this can be achieved by storing most of the NaCl in the vacuole and by synthesizing compatible solutes such as glycine betaine in the cytoplasm, which contribute to maintaining osmotic potential between the cytoplasm and vacuole (Parks et al. 2002, Shen et al. 2002, Wang and

Showalter 2004).

Under the saline conditions observed within the study area, *C. scabrifolia* accumulated similar concentrations of Na^+ and K^+ ions in its leaves. This species showed an efficient regulation of ionic uptake and contained a very high concentration of soluble carbohydrates in order to maintain a sufficiently low osmotic potential in saline habitats. *Phragmites communis* contained a large quantity of K^+ ions in its leaves and accumulated proline and free amino acids in response to salinity stress. In contrast, *S. japonica* and *S. malacosperma* retained high concentrations of inorganic ions to maintain a low water potential and a high ratio of water and tissue succulence in order to avoid ion toxicity by increasing the storage area and diluting accumulated Na^+ and Cl^-. However, they maintained low free amino acid and water soluble carbohydrate contents. These ecophysiological characteristics enable the studied species to grow and adapt to saline environments. Further studies on the interactions of proline, ion contents, and glycine betaine in halophytic plant species are required to elucidate more of these ecophysiological characteristics. Studying the ecophysiological characteristics of halophytes under various environments is essential to select and to improve salt-resistant genes for breeding salt-tolerant plants that are able to withstand salt stresses. In addition, we have to domesticate and introduce halophytes to saline areas where they can be used. At the same time, we should study the various potential economic uses of halophytes.

ACKNOWLEDGMENTS

LITERATURE CITED

Chaplin MF, Kennedy JF. 1994. Carbohydrate Analysis: A Practical Approach. 2nd ed. Oxford University Press, New York, NY, pp 2-3.

Chinnusamy V, Jagendorf A, Zhu JK. 2005. Understanding and improving salt tolerance in plants. Crop Sci 45: 437-448.

Choi SC, Bae JJ, Choo YS. 2004. Inorganic and organic solute pattern of costal plant, korea. Korean J Ecol 27: 355-361.

Choi SC, Lim SH, Kim SH, Choi DG, Kim JG, Choo YS. 2012. Growth and solute pattern of *Suaeda maritima* and

Table 2. Glycine betaine content (µmol/g plant water) in leaves of four halophytic plant species in the study sites between July and September in 2011

	C. scabrifolia	*P. communis*	*S. malacosperma*	*S. japonica*
July	1.65	0.42	1.30	1.67
August	1.07	0.22	1.75	6.19
September	1.77	0.47	1.73	29.84

Suaeda asparagoides in an abandoned salt field. J Ecol Field Biol 35: 351-358.

Choo YS, Albert R. 1997. The physiotype concept: an approach integrating plant ecophysiology and systematics. Phyton 37: 93-106.

Choo YS, Albert R. 1999. Mineral ion, nitrogen and organic solute pattern in sedges (Carex spp.) – a contribution to the physiotype concept. II. Culture experiments. Flora 194: 75-87.

Choo YS, Do JW, Song SD. 1999. Free amino acid and nitrogen contents of the coastal plants in Korea. Korean J Ecol 22: 109-117.

Cramer GR, Lauchli A, Polito VS. 1985. Displacement of Ca^{2+} by Na^+ from the plasmalemma or root cells: a primary response to salt stress. Plant Physiol 79: 207-211.

Di Martino C, Delfine S, Pizzuto R, Loreto F, Fuggi A. 2003. Free amino acids and glycine betaine in leaf osmoregulation of spinach responding to increasing salt stress. New Phytol 158: 455-463.

Flores HE, Galston AW. 1984. Osmotic stress-induced polyamine accumulation in cereal leaves. II. Relation to amino acid pools. Plant Physiol 75: 110-113.

Flowers TJ, Colmer TD. 2008. Salinity tolerance in halophytes. New Phytol 179: 945-963.

Hartzendor T, Rolletschek H. 2001. Effects of NaCl-salinity on amino acid and carbohydrate contents of *Phragmites australis*. Aquat Bot 69: 195-208.

Kefu Z, Hai F, Ungar IA. 2002. Survey of halophyte species in china. Plant Science 163: 491-498.

Khan MA, Ungar IA, Showalter AM. 2000. Effects of salinity on growth, water relations and Ion accumulation of the subtropical perennial halophyte, *Atriplex griffithii var. stocksii*. Ann Bot 85: 225-232.

Kim JH, Cho KJ, Mun HT, Min BM. 1986. Production dynamics of *Phragmites longivalvis, Carex scabrifolia* and *Zoysia sinica* stand of sand bar at the Nagdong river estuary. Korean J Ecol 9: 59-71.

Koyro HW, Zoerb C, Debez A, Huchzermeyer B. 2013. The effect of hyperosmotic salinity on protein pattern and enzyme activities of halophytes. Plant Biol 40: 787-804.

Lee JS. 1988. Studies on the distribution of vegetation in the salt marsh of the Mankyung River estuary. Korean J Environ Biol 6: 1-10.

Lee SH, Ji KJ, An Y, Ro HM. 2003. Soil salinity and vegetation distribution at four tidal reclamation project areas. Korean J Environ Agric 22: 79-86. (in Korean with English abstract)

McCue KF, Hanson AD. 1990. Drought and salt tolerance: towards understanding and application. Trends Biotechnol 8: 358-362.

Min BM and Kim JH. 1999. Plant community structure in reclaaimed land on the West Coast of Korea. J Plant Biol 42: 287-293.

Moghaieb REA, Saneoka H, Fujita K. 2004. Effect of salinity on osmotic adjustment, glycinebetaine accumulation and the betaine aldehyde dehydrogenase gene expression in two halophytic plants, *Salicornia europaea* and *Suaeda maritima*. Plant Sci 166: 1345-1349.

Munns R. 2002. Comparative physiology of salt and water stress. Plant Cell Environ 25: 239-250.

Parida AK, Das AB. 2005. Salt tolerance and salinity effects on plants: a review. Ecotoxicol Environ Saf 60: 324-349.

Parks GE, Dietrich MA, Schumaker KS. 2002. Increased vacuolar Na^+/H^+ exchange activity in *Salicornia bigelovii* Torr. in response to NaCl. J Exp Bot 53: 1055-1065.

Pulich WM. 1986. Variations in leaf soluble amino acids and ammonium content in subtropical seagrasses related to salinity stress. Plant Physiol 80: 283-286.

Qi CH, Chen M, Song J, Wang BS. 2009. Increase in aquaporin activity is involved in leaf succulence of the euhalophyte *Suaeda salsa*, under salinity. Plant Sci 179: 200-205.

Rhodes D, Hanson AD. 1993. Quaternary ammonium and tertiary sulfonium compounds in higher plants. Annu Rev Plant Physiol Plant Mol Biol 44: 357-384.

Rozema J, Flowers T. 2008. Crops for a salinized world. Science 322: 1478-1480.

Shen YG, Du BX, Zhang WK, Zhang JS, Chen SY. 2002. AhCMO, regulated by stresses in *Atriplex hortensis*, can improve drought tolerance in transgenic tobacco. Theor Appl Genet 105: 815-821.

Voetberg GS, Sharp RE. 1991. Growth of the maize primary root at low water potentials. III. Role of increased proline deposition in osmotic adjustment. Plant Physiol 96: 1125-1130.

Wang LW, Showalter AM. 2004. Cloning and salt-induced, ABA-independent expression of choline mono-oxygenase in *Atriplex prostrata*. Physiol Plant 120: 405-412.

Yang HS. 1999. A syntaxonomical study on the vegetation of ruined salt field in Chonnam province. Korean J Ecol 22: 265-270.

Zhu JK. 2001. Plant salt tolerance. Trends Plant Sci 6: 66-71.