

# Importance of Biotic and Soil Factors in Determining the Distribution Strategies of Coastal Salt Marsh Plants

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## Publication Information:

Received 30 October 2020, Accepted 18 November 2020, Available online 22 December 2020

DOI: 10.21463/jmic.2020.09.2.01

## Abstract

The distribution of plant communities in the salt marshes of the southwestern coasts of South Korea was studied, along with environmental or plant factors, by canonical correspondence analysis (CCA) and the competitor (C), stress tolerator (S), and ruderal (R) (CSR) ecological strategies. The coastal salt-marsh plants were classified into three plant-factor groups in the CCA biplot diagram. Group 1 was correlated with LS and FP. Group 2 was correlated with CH and SLA, and Group 3 was correlated with LA, LDMC and LDW. The salt-marsh plants were classified into four soil-factor groups in the CCA biplot diagram. First, the group factor was correlated with TN, TOC, and  $\text{Ca}^{2+}$ . Second, the group factor was distributed according to  $\text{Mg}^{2+}$ , soil texture as Clay and Silt. Third, the group factor was distributed according to Salinity and  $\text{Na}^+$  content. Fourth, the group factor was distributed according to Sand content. To clarify the relative significance of competition, stress, and disturbance in the distribution process of plant communities, the CSR distribution model was adopted. The nine species showed CR (competitor-ruderal) strategies: *Artemisia fukudo*, *Artemisia scoparis*, *Aster tripolium*, *Atriplex gmelinii*, *Imperata cylindrica* var. *koenigii*, *Salicornia europaea*, *Suaeda japonica*, and *Suaeda maritima*. The four species with C (competitor) strategies were *Artemisia capillaris*, *Limonium tetragonum*, *Triglochin maritimum*, and *Zoysia sinica*. *Carex scabrifolia* and *Phragmites communis* displayed SC (stress-tolerant-competitor). Both distribution patterns of the CCA diagrams and CSR triangles may provide a useful scientific basis for protecting and restoring salt marshes and their valuable ecosystem services, considering the increasing disturbances.

## Keywords

salt-marsh plants, plant and soil factor, CCA analysis, CSR strategy

## Introduction

In controlling the distribution of coastal plants, the chemical, physical and biological factors of soil are all believed to play major roles (Ihm and Lee 1998). Because of their transitional situation between sea and terrestrial ecosystems, the southwestern coastal wetlands of South Korea include various habitats, such as salt marshes, salt swamps, and sand dunes (Ihm et al. 2007; Lee and Kim 2018). In many multivariate analyses of coastal wetlands in South Korea, plant communities are arranged along gradients for either soil texture and water potential or soil moisture and soil pH (Lee and Ihm 2004; Shim et al. 2009; Kim et al. 2010). Understanding how global salt marsh plant distribution is caused by abiotic and biotic factors is essential for successful conservation plans in the face of ongoing environmental change (Bertness and Shumway 1993; Bertness and Callaway 1994; Bertness and Hacker 1994; Ihm et al. 2007; Alvarez-Rogel 2007; Kim 2011; Lee and Kim 2018). If the physical and chemical factors of the soil are important attributes conferring a stable distribution, then any perturbations that leave those characteristics relatively unchanged should have little effect on the salt marsh (Pomeroy and Wiegert 1981; Woerner and Hackney 1997; Cho et al. 2017). In general, this seems to be the case, because long-term permanent change in the pattern of tidal flow does affect the vegetation and also the chemical and physical factors of the soil. The frequency of flooding is more important than elevation in predicting marsh-plant zones. Studies done to date indicate that redox potential, ionic composition and moisture content of soil, and latitude, topographical, and climatic factors may play some role in forming vegetation distribution.

Evidence for stable distribution as the result of biological factors or interactions in the salt marshes is more elusive (Pomeroy and Wiegert 1981; Tessier et al 2003; Silander and Antonovics 1982). *Spartina* does have a large biomass of roots and rhizomes and thus has a relatively slow turnover. In fact, the biomass of these reserves is greatest in the high marsh, where potential limits imposed by lack of nutrients are most common. Competition and facilitation are important in mediating zonation, and the importance of facilitation of plant growth increases with increasing physical stress within the abiotic range limits. A refined understanding of facilitation along stress gradients would help inform successful restoration and management of vegetation. In the salt-marsh plant community, a trade-off between belowground competitive ability and the ability to tolerate physical stressors appears to drive plant distribution patterns across the landscape.

Grime (1974) postulated that typical species of three environmental extremes possess distinct factors: competition (C), stress tolerance (S), and ruderal (R). Species position can be plotted in a triangular diagram to indicate their relative importance. Grime (2002), Hodgson et al. (1999), Pierce et al. (2007), and Negreiros et al. (2014) reported that a competitor-ruderal strategy occurred in habitats disturbed by ruderality (a plant's ability to survive in disturbed conditions) and competition. The ratio of ruderalism reflects the dominant disturbance intensity in different habitats. Coastal salt-marsh plant strategies can change from CR to C because of changes from competitor-ruderal to competitor [refer to the location of Fig. 4 (Hodgson et al. 1999)]. Competition also affects the niche differentiation of plant species. More intense disturbance increased functional diversity and species diversity and inhibited dominant stress-tolerator plants. CR plants require rich soil nutrients and, as perennial, biennial or annual plants, can adapt and survive in coastal salt-marsh habitats.

Our research objectives were as follows.

1. We expected that in coastal salt marshes, plants would be classified by disturbance- or stress-tolerant and competition-related variables, and that a higher proportion of the strategies would be near the competition corner of the triangle (ie., CR, C, and SC).
2. Since coastal salt-marsh plant communities have distinct soil environmental features (salinity, pH, etc.), we expected that these differences would show distinct functional strategies and features in Canonical Correspondence Analysis (CCA) Ordinations.
3. We expected that the results in this study would show the relative importance of plant species distribution in CCA ordinations and C, S, and R strategies in coastal salt marshes.

## Methods

We examined several soil environment and plant factors and analyzed them for halophyte distributions of the coastal salt marshes of South Korea (Fig. 1).

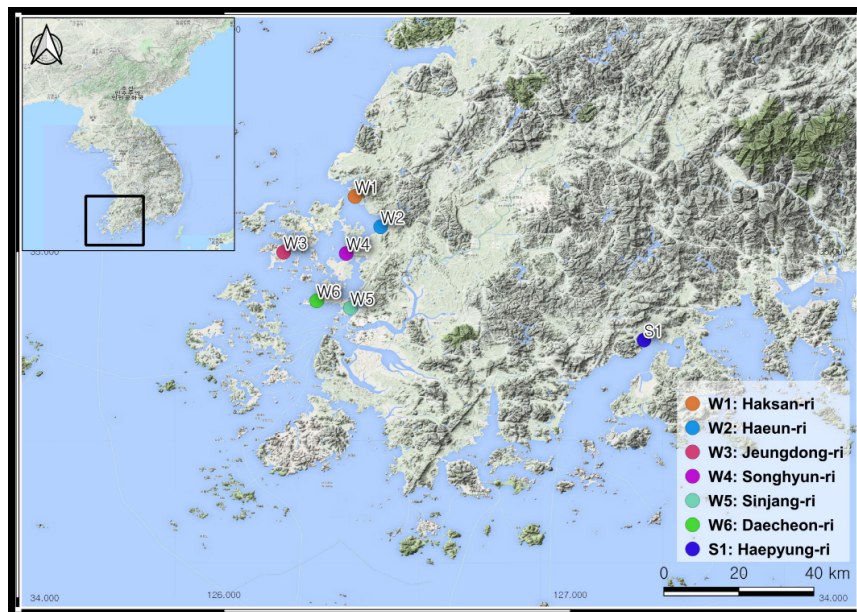


Fig 1. Map of study area of coastal salt marshes of South Korea.

## Study area

Fifteen salt-marsh plant communities were sampled from the west coast to the south coast of South Korea (Fig. 1). The banks of salt marshes were constructed in the study areas. We observed: six west salt marshes and one south salt marsh. The habitat disturbance and status of the study sites are included in Table 1.

Table 1. Study of salt marshes of southwestern coasts in South Korea.

Abbreviation	Local Name of sand dunes	Latitude	Longitude	Habitat status	Dominant community
W1	Haksan-ri	N 35° 09' 33.4"	E 126° 22' 41.9"	Nondisturbed and protected	<i>Suaeda japonica</i>
W2	Haeun-ri	N 35° 04' 18.7"	E 126° 27' 08.5"	Disturbed	<i>Phragmites communis</i>
W3	Jeungdong-ri	N 34° 59' 53.1"	E 126° 10' 19.7"	Protected and nondisturbed	<i>Imperata cylindrica</i> var. <i>koenigii</i>
W4	Songhyun-ri	N 34° 59' 41.0"	E 126° 21' 10.2"	Nondisturbed	<i>Suaeda maritima</i>
W5	Sinjang-ri	N 34° 50' 14.4"	E 126° 21' 54.6"	Beach and disturbed	<i>Artemisia scoparis</i>
W6	Daecheon-ri	N 34° 51' 28.8"	E 126° 16' 04.6"	Disturbed and roadside	<i>Aster tripolium</i>
S1	Haepyung-ri	N 34° 44' 40.9"	E 127° 12' 45.0"	Nondisturbed and protected	<i>Carex scabrifolia</i>

## Plant research by species

We did Canonical Correspondence Analysis (CCA) and the competitor (C), stress tolerator (S), and ruderal (R) (CSR) ecological strategies on 15 species (1 x 1m<sup>2</sup> quadrat, 3 replicates per species) and 19 communities of salt-marsh plants from seven areas July–September 2019 (Table 1). The seven areas and species in them were Haksan-ri, *Zoysia sinica* (Seaside lawngrass); *Limonium tetragonum* (Square-stem statice); *Suaeda japonica* (East Asian seepweed); *Suaeda*

*maritima* (Herbaceous seepweed); Haeun-ri, *Suaeda malacosperma* (Brackish zone seepweed); *Artemisia fukudo* (Asian coastal wormwood); *L. tetragonum* and *Phragmites communis* (Common reed); Jeungdong-ri, *Salicornia europaea* (Marshfire glasswort); *Imperata cylindrica* var. *koenigii* (Blady grass); and *Artemisia capillaris* (Capillary wormwood); Songhyun-ri, *S. maritima* and *Triglochin maritimum* (Sea arrowgrass); Sinjang-ri, *Artemisia scoparia* (Virgate wormwood) and *Carex scabrifolia* (Scabrous-leaf sedge); Daecheon-ri, *Aster tripolium* (Seashore aster); Haepyung-ri, *Atriplex gmelinii* (Gmelin's saltbush); *C. scabrifolia* and *A. fukudo*.

## Soil analysis

We examined the soil environment near the roots at a depth of 15 cm. Air-dried samples (3 replicates per each species) were used for physicochemical analysis (Lee et al. 2020) (Table 4). Soil particle sizes, salinity, total nitrogen, total organic carbon,  $\text{Na}^+$ ,  $\text{Mg}^{2+}$ ,  $\text{Ca}^{2+}$ , and  $\text{K}^+$  were determined by each analyser.

Table 2. Definitions of the predictor variables used the CSR allocation procedure (Hodgson et al. 1999).

Variable	Definition			
CanopyHeight	Six-point classification	1	1–49 mm	
		2	50–99 mm	
		3	100–299 mm	
		4	300–599 mm	
		5	600–999 mm	
		6	>999 mm	
DryMatterContent	Mean of percent dry matter content in the largest, fully hydrated, fully expanded leaves (%)			
FloweringPeriod	Normal duration of flowering period (months)			
FloweringStart	Six-point classification	1	First flowering in March or earlier	
		2	in April	
		3	in May	
		4	in June	
		5	in July	
		6	in August or later, or before leaves in spring	
LateralSpread	Six-point classification	1	Plant short-lived	
		2	Loose tufted ramets radiating about a single axis, no thickened rootstock	in graminoids
		2	Compactly tufted about a single axis, no thickened rootstock	in non-graminoids
		3	Compactly tufted ramets appressed to each other at base	in graminoids
		3	Compactly tufted about a single axis, thickened rootstock present	in non-graminoids
		4	Shortly creeping, <40 mm between ramets	
		5	Creeping, 40–79 mm between ramets	
		6	Widely creeping, >79 mm between ramets	
LeafDryWeight	Natural logarithm of mean dry weight in the largest, fully hydrated, fully expanded leaves (mg), plus 3			
SpecificLeafArea	Mean of area/dry weight quotient in the largest, hydrated, fully expanded leaves (mm <sup>2</sup> /mg)			

## Plant trait analysis

We analyzed several plant factors (Hodgson et al. 1999; Pierce et al. 2013; Lee et al. 2020) (Table 2). The coverage (%), canopy height (CH, mm), lateral spread (LS, mm), leaf area (LA, mm<sup>2</sup>), leaf dry weight (LDW, mg), leaf dry weight/water-saturated fresh mass (LDMC, %), specific leaf area (SLA, mm<sup>2</sup>mg<sup>-1</sup>), flowering period (FP), and flowering start (FS) were measured. We selected a total of 15 shrub and herbaceous species for the measurements of plant functional factors.

## Statistical analyses

Significance of differences in plant factors (Table 3) and in soil factors (Table 4) among the samples were tested with one-way ANOVA. We did CCA analyses of soil factors and plant factors by using CANOCO 5.1 (Ter Braak 1986; Ter Braak and Smilauer 2018; Lee et al. 2020). The CSR strategies were chosen using plant functional factors and the triangular diagrams generated according to Hodgson et al. (1999) and Pierce et al. (2013), using SigmaPlot 13 (www.sigmaplot.com).

Table 3. Summary statistics of plant traits. One-way ANOVA results showed significant differences of all plant traits among plant communities ( $df = 14$ ,  $p < 0.001$ ).

	Canopy height (mm)	Leaf dry matter content (%)	Flowering period (# of months)	Lateral spread (six-point model)	Leaf dry weight (mg)	Specific leaf area (mm <sup>2</sup> mg <sup>-1</sup> )	Flowering start (month)
Means	380	18	2	2	784	2	5
SD	215	13	0	1	982	2	1
N	15	15	15	15	15	15	15
MAX	700	44	3	3	3840	8	6
MIN	150	6	2	1	97	0	3
Range	550	37	1	2	3743	7	3

Table 4. Summary statistics of soil factors. One-way ANOVA results showed significant differences of all soil factors among plant communities ( $df = 14$ ,  $p < 0.001$ ).

	Salinity (psu)	T-N (mg/kg)	TOC (%)	Ca <sup>2+</sup> (cmol/kg)	K <sup>+</sup> (cmol/kg)	Mg <sup>2+</sup> (cmol/kg)	Na <sup>+</sup> (cmol/kg)	Sand (%)	Silt (%)	Clay (%)
Means	1.025	526.0	0.945	75.556	31.172	45.587	159.6	93.7	3.713	2.543
SD	1.037	331.8	0.679	85.463	18.627	29.934	154.7	8.0	4.523	3.465
N	15	15	15	15	15	15	15	15	15	15
MAX	3.052	1109.5	3.033	343.203	60.207	91.437	448.1	99.9	15.816	11.350
MIN	0.092	124.5	0.317	5.361	5.958	7.528	13.9	72.8	0.062	0.020
Range	2.961	985.1	2.716	337.842	54.248	83.909	434.2	27.1	15.754	11.330

## Results

The most abundant species (Table 5) in this study was *Artemisia fukudo* and *Imperata cylindrica* var. *koenigii*; (cover = 100%), which exhibited a CR (competitor-ruderal strategy) (C:S:R = 58.8:0.0:41.2; C:S:R = 58.1:0.0:41.9). The second most abundant species (*Carex scabrifolia* and *Phragmites communis*; cover = 100%) exhibited an SC (stress-tolerant-competitor) strategy (C:S:R = 53.2:46.8:0.0; C:S:R = 56.3:43.7:0.0). The third most abundant species (*Triglochin maritimum* and *Zoysia sinica*; cover = 100%) demonstrated C (C:S:R = 88.5:0.0:11.5; C:S:R = 100.0:0.0:0.0). One-way ANOVA results showed significant differences of all plant factors and soil factors among the plant communities ( $df = 14$ ,  $p < 0.001$ ).

Table 5. Plant species, their C(%), S(%), R(%) percentages, and CSR strategies from Hodgson et al. (1999) and Caccianiga et al. (2006) collected from the sand-dune communities of the southwestern coast in Korea.

Species	Percentage from Hodgson et al. (1999)			Strategy type	Percentage from Caccianiga et al. (2006)			Strategy type	Plant cover (%)
	C(%)	S(%)	R(%)		C(%)	S(%)	R(%)		
<i>Artemisia capillaris</i>	100.0	0.0	0.0	C	100.0	0.0	0.0	C	90
<i>Artemisia fukudo</i>	58.8	0.0	41.2	CR	59.0	0.0	41.0	CR	100
<i>Artemisia scoparis</i>	55.8	0.0	44.2	CR	56.2	0.0	43.8	CR	90
<i>Aster tripolium</i>	50.9	0.0	49.1	CR	51.7	0.0	49.3	CR	50
<i>Atriplex gmelinii</i>	58.1	0.0	41.9	CR	57.5	0.0	42.5	CR	80
<i>Carex scabrifolia</i>	53.2	46.8	0	SC	52.8	47.2	0.0	SC	100
<i>Imperata cylindrica</i> var. <i>koenigii</i>	58.1	0.0	41.9	CR	57.5	0.0	42.5	CR	100
<i>Limonium tetragonum</i>	96.0	0.0	4.0	C	94.7	0.0	5.3	C	50
<i>Phragmites communis</i>	56.3	43.7	0.0	SC	56.5	43.5	0.0	SC	100
<i>Salicornia europaea</i>	51.4	0.0	48.6	CR	51.4	0.0	48.6	CR	70
<i>Suaeda japonica</i>	57.6	0.0	42.4	CR	58.7	0.0	41.3	CR	70
<i>Suaeda malacosperma</i>	48.6	0.0	51.4	CR	48.8	0.0	51.2	CR	60
<i>Suaeda maritima</i>	51.4	0.0	48.6	CR	52.2	0.0	47.8	CR	80
<i>Triglochin maritimum</i>	88.5	0.0	11.5	C	88.5	0.0	11.5	C	100
<i>Zoysia sinica</i>	100.0	0.0	0.0	C	25.9	74.1	0.0	S/SC	70

Fifteen of the 19 species were allocated to CR, C, and SC strategies (Table 5 and Fig. 5). They displayed competition and disturbance adaptation strategies reflecting the ecological environment (Lee et al. 2020). In the study area, 9 species showed CR (competitor-ruderal) strategies; these were *Artemisia fukudo*, *Artemisia scoparis*, *Aster tripolium*, *Atriplex gmelinii*, *Imperata cylindrica* var. *koenigii*, *Salicornia europaea*, *Suaeda japonica*, *Suaeda malacosperma*, and *Suaeda maritima* (Table 5 and Fig. 5). They had 0.17–2.55 mm<sup>2</sup>/mg SLA and 150–700 mm canopy height. Some of them had rhizomes and lateral vegetative growth and showed CR strategies in disturbed salt marshes. The four species with C strategies were *Artemisia capillaris*, *Limonium tetragonum*, *Triglochin maritimum*, and *Zoysia sinica* (Fig. 5). Meanwhile, *Carex scabrifolia* and *Phragmites communis* displayed SC (stress-tolerant-competitor) strategies.



Figure 2 shows the canonical correspondence analysis (CCA) bi-plot diagram of coastal salt marshes in the southwestern coasts of South Korea. Axes 1 and 2 are the vegetation plots and the plant factors. The plant factors are shown as arrows. The 15 plant communities, classified into three groups, are displayed on axes 1 and 2. Group 1 was correlated with LS and FP (Table 6). Group 2 was correlated with CH and SLA, and Group 3 was correlated with LA, LDMC and LDW. The total variation was 12.70, and explanatory variables accounted for 56.39% of the variation. The eigenvalues of axes 1 and 2 were 1.0000 and 0.9955, and those of axes 3 and 4 were 0.8859 and 0.7274, respectively. The explained variations (cumulative) of axes 1 and 2 were 7.88 and 15.72, respectively.

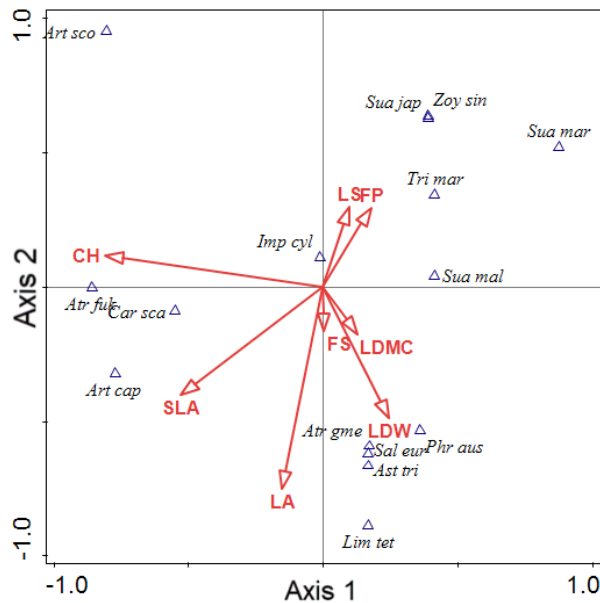


Fig 2. Canonical correspondence analysis (CCA) bi-plot diagram.

Note: Axes 1 and 2 are the vegetation plots and the plant-factor variables. Plant-factor variables are shown as arrows. The arrows point in the direction of plant factors with the highest values in the vegetation plots. The lengths of the arrows are proportional to their importance in explaining the species variation.

Art cap = *Artemisia capillaris*; Art fuk = *Artemisia fukudo*; Atr sco = *Artemisia scoparis*; Atr tri = *Aster tripolium*; Atr gme = *Atriplex gmelinii*; Car sca = *Carex scabrifolia*; Imp cyl = *Imperata cylindrica* var. *koenigii*; Lim tet = *Limonium tetragonum*; Phr com = *Phragmites communis*; Sal eur = *Salicornia europaea*; Sua jap = *Suaeda japonica*; Sua mal = *Suaeda malacosperma*; Sua mar = *Suaeda maritima*; Tri mar = *Triglochin maritimum*; Zoy sin = *Zoysia sinica*.

Table 6. Eigenvalues, explained variation, pseudo-canonical correlations, and explained fitted variation in CCA of 15 relevées, 15 response plant species, and 8 explanatory plant variables.

Statistic	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	1.0000	0.9955	0.8859	0.7274
Explained variation (cumulative)	7.88	15.72	22.69	28.42
Pseudo-canonical correlation	1.0000	0.9995	0.9936	0.9699
Explained fitted variation (cumulative)	13.97	27.87	40.24	50.40



Figure 3 presents the CCA ordination results of the coastal plant dataset. The 15 community scores are plotted along axes 1 and 2 and clustered into four groups. The CCA eigenvalues for the first two ordination axes were 1.0000 and 1.0000 (Table 7). The explanatory variables accounted for 63.27% of the variance in the community data. First, the group factor was correlated with TN, TOC, and  $\text{Ca}^{2+}$ . Second, the group factor was distributed according to  $\text{Mg}^{2+}$ , soil texture as Clay and Silt. Third, the group factor was distributed according to Salinity and  $\text{Na}^{+}$  content. Fourth, the group factor was distributed according to Sand content.

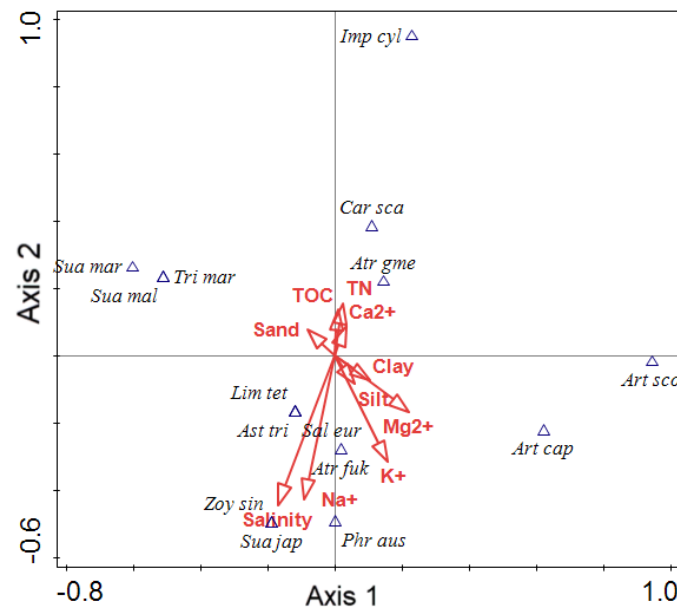


Fig 3. Canonical correspondence analysis (CCA) bi-plot diagram. The 15 community scores were plotted along Axes 1 and 2 and can be clustered into the four factor groups. Soil factors are shown as arrows. See Fig. 2 for species names.

Table 7. Eigenvalues, explained variation, pseudo-canonical correlation, and explained fitted variation in CCA of 15 relevées, 15 response plant species, and 10 explanatory soil variables.

Statistic	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	1.0000	1.0000	1.0000	1.0000
Explained variation (cumulative)	7.88	15.75	23.63	31.50
Pseudo-canonical correlation	1.0000	1.0000	1.0000	1.0000
Explained fitted variation (cumulative)	12.45	24.90	37.35	49.80

## Discussion

In this article, one of our intent was to identify the CSR strategies of salt-marsh plants. In this study, plant-factor measurements and Braun-Blanquet's vegetation classification (1964) were useful for coastal-plant ecosystem conservation in South Korea (Townend et al. 2010, Gu et al. 2018). Ihm and Lee (1998) reported that, to describe the major environmental factors operating in coastal wetlands and to characterize the distribution of the plant species over

the coastal wetlands, 12 physical and chemical properties of the soil were assessed. The gradient of water and osmotic potential of the soil, electrical conductivity, sodium and chloride content, and soil texture along the three habitat types of salt marshes, salt swamp, and sand dunes were found. The 24 coastal-plant communities from principal component analysis (PCA) on the 12 variables were designated as a gradient for soil texture and water potential related to salinity by Axis 1 and as a gradient for soil moisture and total nitrogen by Axis 2. Those on Axis 1 were divided into 3 groups: (1) 9 salt-marsh communities, including *Salicornia herbacea*; (2) 5 salt-swamp communities, including *Scirpus fluviatilis*; and (3) 10 sand-dune communities, including *Imperata cylindrica*. Those on Axis 2 were divided into 2 groups: (1) salt-marsh and sand-dune communities, and (2) 3 salt-swamp communities. The results could account for the zonation of plant communities on coastal wetlands observed along environmental gradients.

In the diagram produced by CCA, the pattern of ordination was consistent with that of our DCA results (Lee et al. 2012). The communities were arranged into two groups of sand-dune and other vegetation along Axis 1, as well as two groups of salt-marsh plus salt-swamp vegetation along Axis 2. CCA Axis 1 displayed soil water and osmotic potential, soil moisture content, electrical conductivity, and organic matter gradient. In all, 14.9% of the variance among species data could be explained by the two CCA axes. These low values could be attributed to the high noise levels typical of species-abundance data (ter Braak, 1986).

**Abiotic factors** (Lee and Kim 2018): Understanding salt-marsh plant distribution and zonation is essential for successful conservation and restoration plans in the face of ongoing environmental change (Bertness and Ellison 1987; Pennings and Callaway 1996; Min and Kim 1999; Kim 2005; Engels and Jensen 2010; Lee and Kim 2018). The results of studies by Bertness and Ellison (1987) and Pennings and Callaway (1996) indicate that salt-marsh plants tend to cluster into various vegetation groups because of the combination of abiotic and biotic factors and positive feedback. These are, first, flooding frequency; second, soil moisture content; third, salinity; fourth, geographical variations in the physical environment; and fifth, spatial heterogeneities in soil properties.

**Biotic factors** (Lee and Kim 2018): Besides various chemo-physical factors, the biotic influences are important for understanding the pattern of halophyte distribution. These are, first, competition and facilitation; second, a trade-off between belowground competitive ability and the ability to tolerate the physical stressors; third, salt tolerance; fourth, the early seedling establishment phase; fifth, grazing; sixth, *Spartina densiflora* alters native zonation patterns via invasion of *Spartina maritima* tussocks into areas that should be occupied by native species.

Fifteen of the 19 species were allocated to CR, C, and SC strategies. They displayed competition and disturbance adaptation strategies reflecting the ecological environment (Lee and Kim 2018; Lee et al. 2016; Lee et al. 2020). In the study area, 9 species showed CR (competitor-ruderal) strategies: *Artemisia fukudo*, *Artemisia scoparis*, *Aster tripolium*, *Atriplex gmelini*, *Imperata cylindrica* var. *koenigii*, *Salicornia europaea*, *Suaeda japonica*, *Suaeda malacosperma* and *Suaeda maritima* (Table 4 and Fig. 5). Some of them had rhizomes and lateral vegetative growth and showed CR strategies in disturbed salt marshes. The four species with C strategies were *Artemisia capillaris*, *Limonium tetragonum*, *Triglochin maritimum*, and *Zoysia sinica*. Meanwhile, *Carex scabrifolia* and *Phragmites communis* displayed SC (stress-tolerant-competitor) strategies. Distribution research on biotic factors and abiotic factors is especially important for restoration and conservation plans considering environmental changes (Lee and Kim 2018). To date, the vegetation establishment of coastal salt marshes has been related to salinity in the soil and seawater, redox potential, the soil ion composition, and soil moisture content. CCA showed that the distributions of invasive native and exotic species were significantly segregated, according to the disturbance level, exotic species number, gravel, sand, and silt contents, and

vegetation size (Kim 2005; Lee and Kim 2018; Fig. 4 and Fig. 5). We also found that human disturbance strongly favored the settlement of invasive and exotic species.

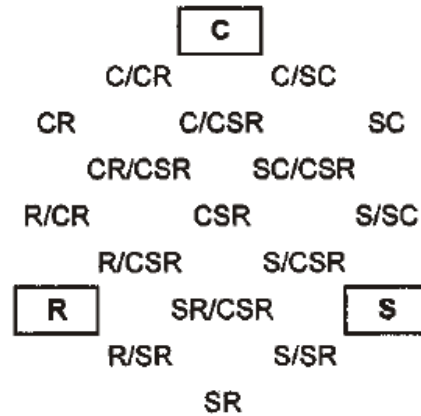


Fig 4. The location of 19 plant functional types in C-S-R space.

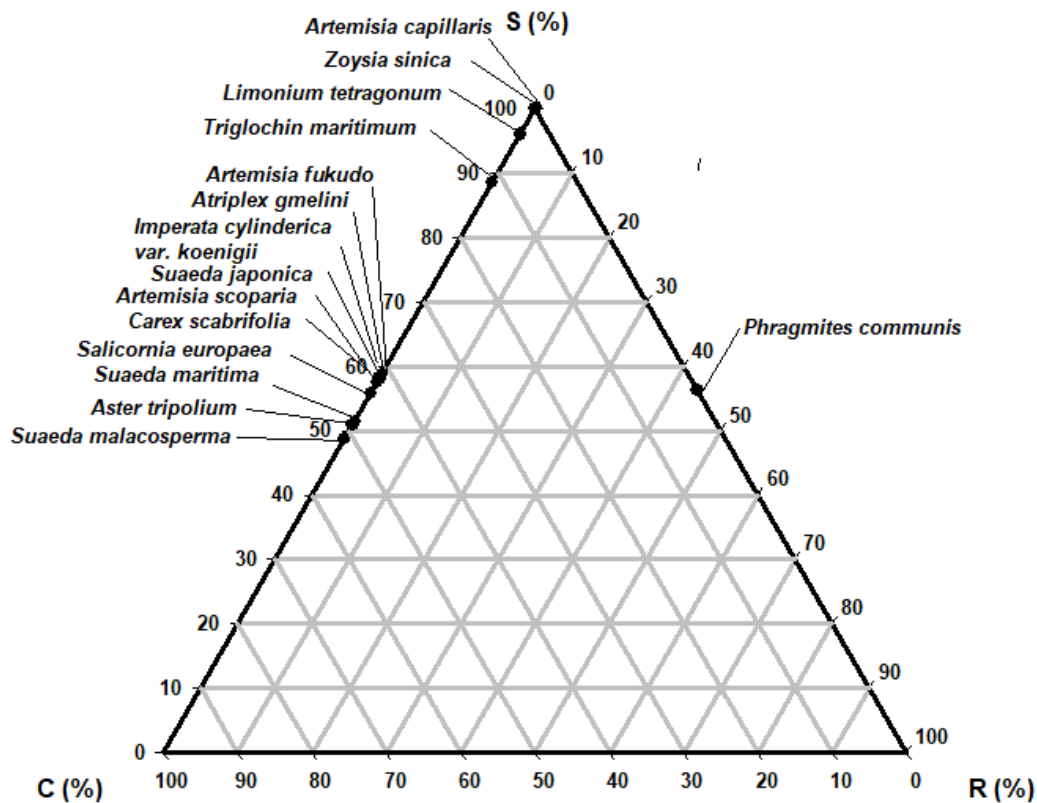


Fig 5. Competitive, stress-tolerant, and ruderal (CSR) classification by 8 plant factors from Hodgson et al. (1999) and Pierce et al. (2013) of 15 plant species in coastal salt-marsh plant communities from the south-western coast of South Korea.

## Conclusions

The coastal salt-marsh plants were classified into three plant-factor groups in the CCA biplot diagram. The 15 plant communities, classified into three groups, are displayed on axes 1 and 2. Group 1 was correlated with LS and FP (Table 6). Group 2 was correlated with CH and SLA, and Group 3 was correlated with LA, LDMC and LDW. The plants were classified into two soil-factor groups in axes 1 and 2 of the CCA biplot diagram. First, the vegetation was correlated with total organic carbon (TOC), total nitrogen (T-N), and  $\text{Ca}^{2+}$ . Second, it was correlated with the salinity,  $\text{Na}^+$ , and  $\text{K}^+$ . To clarify the relative significance of competition, stress, and disturbance in the distribution process of plant communities, we adopted the CSR distribution model. The nine species showed CR (competitor-ruderal) strategies. Both distribution patterns of the CCA diagrams and CSR triangles may provide a useful scientific basis for protecting and restoring salt marshes and their valuable ecosystem services, in the face of increasing disturbances.

## Acknowledgments

This research was supported by the Basic Science Research Program through the National Research Foundation of Korea (NRF) funded by the Ministry of Education of Korea (NRF-2018R 1D 1A 1B06043748).

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