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Plant distribution along an elevational gradient in a macrotidal salt marsh on the west coast of Korea

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ABSTRACT

The distribution of halophytes in salt marshes is generally determined by environmental gradients, and it is important to identify the principal factors involved. This study recorded how marsh plants, which have received limited attention, were distributed along elevational gradients, and investigated the environmental factors affecting their distribution on the Siheung Tidal Flat, which has one of the largest tidal ranges in the world. Plant and soil samples were collected in September 2015 from 203 plots that had been randomly selected in the intertidal zone. Soil salinity in the high-elevation plots varied over a wide range. Each halophyte species had a distinct zonation according to elevation. Cluster analysis classified plots into four clusters reflecting plant community composition (Cluster 1 at high elevation, defined by *Suaeda glauca*, *Zoysia sinica*, and *Phragmites australis*; Cluster 2 at mid-high elevation, defined by *Phacelurus latifolius*; Cluster 3 at low elevation, defined by *Suaeda japonica*; Cluster 4 at mid-high elevation, defined by *Carex scabrifolia*). Non-metric multidimensional scaling indicated that the distribution of *S. japonica* was strongly influenced by elevation and flood frequency, whereas that of *P. latifolius* was negatively influenced by soil salinity and soil cations (Na^+, Mg^{2+}, K^+, Ca^{2+}). Understanding the relationship between halophyte distribution and environmental factors along elevational gradients in a natural salt marsh provides important ecological information that may contribute to salt marsh restoration.

1. Introduction

The distribution of salt marsh plants is generally determined by environmental gradients, including those caused by physicochemical and biotic factors such as tidal inundation, variations in salinity, and interactions with other species (Ungar, 1998). Surface elevation and tidal inundation are among the main drivers of halophyte distribution (Bertness, 1991; Adam, 1993; Rasser et al., 2013). In salt marshes, topographic features formed by the tides, such as channels, levees, and ponds, are irregularly distributed (Stribling et al., 2007). The resulting topographic heterogeneity results in elevational variations in surface microtopography. In salt marshes, small changes in elevation can affect plant occurrence and distribution by affecting the level of waterlogging in soil (Varty and Zedler, 2008). Changes in elevation have a direct influence on flood frequency and inundation time, and can indirectly affect other environmental factors (Davy et al., 2011; Castillo et al., 2000). At lower elevation, flood frequency and inundation time increase, low oxygen content generates a reducing state in the soil, and halophytes must be able to tolerate anaerobic conditions (Colmer and Flowers, 2008). Although the tide provides water and nutrients to salt marsh plants (Steever et al., 1976), it can affect their distribution by flooding and by increasing salinity stress (Detling and Klikoff, 1973; Flowers and Colmer, 2015).

Soil salinity in salt marshes is often influenced by elevation (Pennings et al., 2005), but also by other environmental factors. Flood frequency varies with elevation, with consequent effects on exposure time, temperature, and solar radiation, all of which affect soil water evaporation and salinity (Pennings et al., 2005). Soil salinity can also vary depending on fresh water inputs (Wang et al., 2017) and the presence of halophytes (Pennings and Bertness, 1999), which may influence soil nutrient concentrations. Salt marsh plants in high-salinity regions make limited use of water absorption via osmotic pressure, and their growth and biomass are limited by salt stress, which affects photosynthesis, protein synthesis, and energy metabolism (Debez et al., 2004; Parida and Das, 2005). Salt marsh plant species can survive in soils with widely different salinities, as they have different salt tolerance ranges and adaptation strategies. Therefore, understanding how environmental factors and marsh plant distribution varies with elevation can reveal how each species responds to physico-chemical environmental factors and provide important information on key factors

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determining plant distribution and productivity.

The distribution of halophytes in salt marshes can also be affected by interspecific competition, commensalism and other interspecific interaction along the development of ecological succession (Figueroa et al., 2003). Generally, the lower limit of a species distribution may be determined by tide-related abiotic factors, whereas interspecific competition may be an important biological factor affecting plant distribution in the upper intertidal zone (Crain et al., 2004). However, Pennings and Callaway (1992) showed that interspecific competition may not be the sole factor determining halophyte distribution in the upper intertidal zone. Distribution and abundance of salt marsh plants can be measured using a variety of indices such as biomass, cover, and frequency. Plant cover is easy to record, but the error range between individual samples can be large depending on the sampling technique and the number of samples (Hanley, 1978). By contrast, plant biomass can be measured by anyone using an electronic balance, and small individual samples can be measured accurately. Statistical analysis of biomass data can clarify the relationship between vegetation distribution and environmental factors and how these vary with elevation.

Recently, the total area covered by tidal flats in South Korea has decreased rapidly due to human activities, such as the construction of sea walls and harbors and reclamation projects converting salt marshes to agricultural and industrial land (Hong et al., 2010). The total area of tidal flats has been reduced from an estimated 3900 to 2400 km^2 over 30 years (Park et al., 2015). This habitat loss and the resulting disturbance has impacted plant communities, migratory birds, and other mudflat organisms. Several factors have led to a recent growth of interest in salt marsh restoration. Salt marshes provide a protective buffer zone against tsunami waves, storms (hurricanes), and sea level rise (Moeller et al., 1996; Wolters et al., 2005). Tidal flat ecosystems are highly productive, and restoration may promote coexistence between humans and the natural environment (Wolters et al., 2005). Despite the increased interest in salt marsh restoration, most studies have focused on vegetation establishment and development (Warren et al., 2002). For successful restoration, it is also important to monitor the structure and function of the original ecosystem. The ultimate goal of wetland restoration is to create a sustainable and naturally functioning ecosystem. However, the success of salt marsh restoration is still controversial. One reason is the limited monitoring information on natural ecosystems (Zhao et al., 2016). Monitoring natural salt marshes is essential to provide reference data for restoration. Understanding the relationship between halophyte distributions and physical environmental factors, especially elevation, is an important key to salt marsh restoration (Williams and Faber, 2001) and may also provide important data on the potential effects of sea level rise.

The distribution of salt marsh plants is expected to vary depending on the region and natural conditions. The Siheung Tidal Flat has one of the largest tidal ranges (from 4 to 9 m) in the world and is one of the typical salt marshes of the west coast of Korea (Wells et al., 1990). Despite its ecological importance, there are no data on marsh plant distributions in relation to elevation in this part of Korea. This study therefore aimed to address the question of how environmental factors affect halophyte distributions on the Siheung Tidal Flat. We tested two hypotheses: (1) each salt marsh plant species has a different distribution range with respect to elevation; (2) elevation, flood frequency, salinity, available phosphorus and soil cations (Na^+, Mg^{2+}, K^+, Ca^{2+}) significantly influence salt marsh plant distribution and biomass. To test our first hypothesis, we recorded the distribution range of seven salt marsh plant species in the intertidal zone of the Siheung Tidal Flat using quadrats and precise measurements of elevation. To test the second hypothesis, we calculated the flood frequency based on the elevations measured at each plot on the Siheung Tidal Flat, and conducted a quantitative field survey to sample vegetation and soil environmental factors.

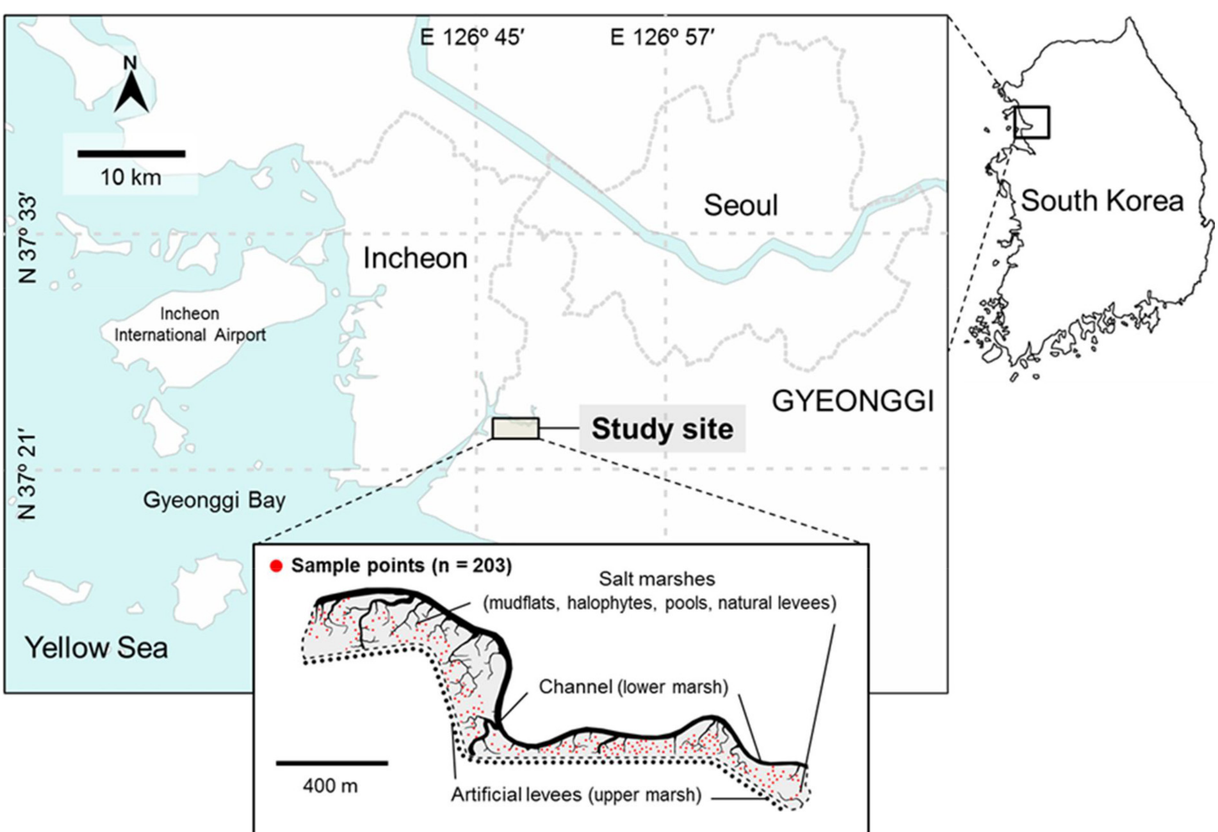

Fig. 1. Map showing the location of the study site and sampling plots (n = 203), Siheung Tidal Flat, on the west coast of South Korea.

2. Material and methods

2.1. Study site

The field study was conducted at Siheung Tidal Flat (37° 23′ 40″ N, 126° 46′ 05″ E), which is located in the back bay at Gyeonggi Bay, facing the Yellow Sea in South Korea. Siheung Tidal Flat (~0.71 km^2) was designated a Coastal Wetland Protected Area in 2012 and consists of salt marsh, mudflats, and tidal channels (Fig. 1). The tidal channels, a major feature of this wetland, are formed as a result of the high tidal range (from 4 to 9 m), and facilitate the movement of seawater (Wells et al., 1990). The study area is located in the temperate climatic zone. Mean annual temperature is 12.1 °C, and annual precipitation is 1234 mm. Most rainfall occurs from June to September, this period accounting for 70% of the total annual precipitation (Korea Meteorological Administration, http://www.kma.go.kr/).

Suaeda japonica Makino (Chenopodiaceae) forms the dominant vegetation at the study site. This annual plant is widely distributed throughout the west coast of Korea and can tolerate wide ranges of waterlogging and salinity (Hayakawa and Agarie, 2010). Another dominant plant is the perennial *Phacelurus latifolius* Ohwi (Gramineae). *Phragmites australis* Trin ex Steud (Gramineae), *Suaeda glauca* Bunge (Chenopodiaceae), *Carex scabrifolia* Steudel (Cyperaceae), *Artemisia fukudo* Makino (Asteraceae), and *Zoysia sinica* Hance (Poaceae) are less common at the study site than *S. japonica* and *P. latifolius*.

2.2. Field survey

The field survey was conducted in September 2015. Two hundred and three sampling plots (1 × 1 m) were randomly selected across the site, including the seven dominant salt marsh plants and bare ground at various elevations (Fig. 1). Each plot was installed over 10 m away from any adjacent plots to avoid spatial autocorrelation (Schlesinger et al., 1996). All samples were collected from 203 plots in the intertidal zone where halophytic plants grow in the study area (Fig. 2). At each sampling point, the relative elevations of the plots in the intertidal zone were measured with a height accuracy of < 2.0 mm using a digital level instrument (DL-200, South, China). Then, the elevations reached by high tide in the study area were obtained from real-time tide observations (absolute elevation value; m) provided by the Korea Ocean Observing and Forecasting System (KOOFS), which relate to the Korea original bench mark. After installing PVC pipes perpendicular to the ground at the points of high tides, the relative elevations of the points of high tide in the study area were also measured using a digital level instrument (DL-200, South, China). All relative elevation values were then converted to absolute elevation values using the information provided by KOOFS for the study area. Flood frequency was calculated using the following method: the high tide elevation value during tidal period > the elevation value at each plot = 1 (flood frequency). The flood frequency at each sampling plot was calculated using the database (1 year of data) of the Korea Hydrographic and Oceanographic Agency, which provided Automated Real-Time Tidal Elevation information (absolute elevation value; m) for the study area.

The vegetation survey carried out in each plot measured above-ground fresh biomass, frequency of occurrence, and percentage cover of each plant species. The percentage cover of all plant species was recorded to the nearest 5%, except for rare species (nearest 1%). The percentage cover of bare ground was also recorded. Above-ground fresh biomass was measured on September 24th, 2015, and soil samples were taken on September 23rd, 2015, at the lowest tide periods in September to eliminate the influence of tide and precipitation. Soil samples were taken from five random subsamples at 5 cm depth in each plot. The five subsamples representing each plot were mixed completely (~500 ml volume per sample) and then stored in a sealed plastic bag at 4 °C until soil analysis was conducted.

2.3. Soil analysis

In each of the 203 soil samples, water content was calculated by measuring the difference in sample weight (10 g) before and after heating in an oven at 105 °C for 48 h. Organic matter content was determined by the loss-on-ignition method (John, 2004). To measure soil pH and soil salinity, air-dried soil samples were passed through 2 mm sieves and mixed with distilled water (1:5) for 1 h. Soil pH and electrical conductivity were then measured using a multiparameter bench meter (PC2700, Eutech, Singapore). The electrical conductivity was converted into salinity using the formula, Salinity (ppt) = 0.064 × EC × (% water in soil/100) × 10, where EC = Electrical conductivity (m mho cm^{-1}) (Joshi and Ghose, 2003). The cations Na^+, Mg^{2+}, K^+, and Ca^{2+} were determined by the Mehlich-3 extraction method (Ziadi and Tran, 2007) and measured using an Inductively Coupled Plasma Emission Spectrometer (ICP-730ES, Varian, Australia). Soil available phosphorus was extracted by Mehlich-3 solution and measured using colorimetry (Ziadi and Tran, 2007).

2.4. Data analysis

Three analysis steps were conducted in R software (R Development Core Team, 2016) in order to relate variation in salt marsh plant communities to environmental factors. Nonparametric statistics were used because of non-normality of the data. Firstly, to identify patterns of similarity in plant community structure, a cluster analysis (CA) based on species biomass data was computed. Cluster analysis was performed using the UPGMA linkage method and the Bray-Curtis dissimilarity matrix. Multi-response permutation procedures were applied to check for significant differences between the clusters. Secondly, Kruskal-Wallis tests were conducted to evaluate variation in environmental factors and plant community structure in the different clusters identified by CA. Multiple comparison tests were then performed using the *kruskalmc* function in the *pgirmess* package if there were significant

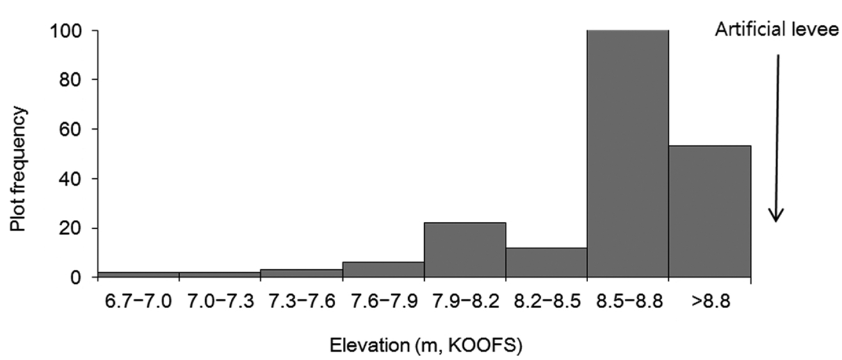

Fig. 2. Frequency, according to elevation, of the 203 sampling plots (1 × 1 m) on the Siheung Tidal Flat in 2015. Elevation data from the Korea Ocean Observing and Forecasting System (KOOFS).

Table 1
Environmental factors measured at each of the 203 study plots at SiheungTidal Flat in Korea. Elevation data from the Korea Ocean Observing and Forecasting System (KOOFS).

Variables	Mean	Standard error	Range
Elevation (m)	8.59	0.03	6.76–9.13
Flood frequency (no. of days $year^{-1}$)	109	7	583–19
Soil water content (%)	30.8	0.7	12.5–79.0
Soil organic matter (%)	4.9	0.1	2.8–8.7
Soil pH	7.08	0.03	6.24–8.24
Soil salinity (ppt)	8.64	0.22	3.31–16.99
Soil Na^+ ($mg\,g^{-1}$)	11.79	0.32	4.59–26.40
Soil Mg^{2+} ($mg\,g^{-1}$)	2.41	0.05	1.21–4.34
Soil K^+ ($mg\,g^{-1}$)	1.11	0.01	0.70–1.74
Soil Ca^{2+} ($mg\,g^{-1}$)	0.79	0.01	0.42–1.51
Soil available phosphorus ($mg\,g^{-1}$)	0.06	0.002	0.02–0.14

differences in the Kruskal-Wallis test ($P < 0.05$). Thirdly, non-metric multidimensional scaling (NMS) was used based on Bray-Curtis distances between sampling sites. The 'vegan' package in R was applied for NMS computation. In this package, the function 'metaMDS' was used to find the best solution with the lowest stress value (Bae et al., 2014), and the function '*envfit*' was then used to evaluate the relationships between the salt marsh plant community and environmental factors.

3. Results

3.1. Environmental factors

Flood frequencies in the lowest (+6.67 m) and highest (+9.13 m) elevation plots in the study area were 583 and 19 inundations per year, respectively, an almost 30-fold difference (Table 1). Soil water content decreased significantly with increasing elevation, ranging from 12.5% to 79.0% ($r = -0.488$, $n = 203$, $P < 0.001$).

Although soil salinity did increase with elevation, there was substantial variation, particularly at high elevations (+8.5 to +9.0 m) (Fig. 3a). Soil available phosphorus was negatively correlated with elevation ($r = -0.675$, $n = 203$, $P < 0.001$). Available phosphorus values were high at low-elevation plots, and decreased strikingly with increases in elevation (Fig. 3b). Na^+ and Mg^{2+} were both positively correlated with elevation ($r = 0.194$, $n = 203$, $P < 0.010$ and $r = 0.083$, $n = 203$, $P = 0.239$ respectively), whereas K^+ and Ca^{2+} were negatively correlated with elevation ($r = -0.164$, $n = 203$, $P < 0.050$ and $r = -0.242$, $n = 203$, $P < 0.001$, respectively).

3.2. Plant distribution

Suaeda japonica and *P. latifolius* were the most common plant species, accounting for 40% of the total cover at the study site. There was also much bare ground (Table 2). The distribution of bare ground and the seven plant species differed according to elevation and soil salinity (Fig. 4). Spatial extent of bare ground was 100% at the lowest elevation, declining with increasing elevation as plants appeared (Fig. 4o). Despite some differences in distribution, all plant species occurred at elevations above +7.0 m. *Suaeda japonica* and *C. scabrifolia* showed unimodal distributions, with their peak biomass at +8.2 to +8.5 m and +8.5 to +8.8 m, respectively (Fig. 4c and m). *Zoysia sinica* and *P. latifolius* (Fig. 4a and k) became gradually more abundant with increasing elevation, reaching maximum biomass in the highest elevation plots (above +8.8 m). *Phragmites australis* and *S. glauca* were absent in plots at elevations below +8.5 m, and had peak abundance at +8.5 to +8.8 m (Fig. 4e and i).

Plant distribution patterns relative to soil salinity were the inverse of those seen with respect to elevation. The percentage of bare ground was relatively low in low-salinity plots, and tended to increase progressively with increasing salinity (Fig. 4p). With the exception of *C. scabrifolia* and *S. japonica*, the maximum biomass of plant species coincided with low soil salinity (cf. *Z. sinica* and *P. australis* 3–5 ppt; *A. fukudo* and *P. latifolius* 5–7 ppt; *S. glauca* 7–9 ppt) (Fig. 4b, f, h, l and j). *Suaeda japonica*, the most common plant, is well-adapted to a high-salinity waterlogged environment, and occurred at a wide range of salinities (Fig. 4n). Biomass of *P. latifolius* tended to be high in low-salinity plots, and declined steeply with increasing salinity, especially at > 7 ppt (Fig. 4l). Biomass of *Z. sinica* and *P. australis* peaked at low salinity (Fig. 4b and f), and that of *C. scabrifolia* peaked at high salinity (Fig. 4d). *Suaeda glauca* peaked at low-mid salinity, whereas *A. fukudo* was not found at salinities > 9 ppt (Fig. 4h and j).

Cluster analysis of plots based on plant community composition (Fig. S1) identified four clusters (1–4) related to variation in environmental characteristics (Table 3). *Suaeda japonica* was dominant in Cluster 3, associated with the lowest elevation and highest flood frequency ($P < 0.050$). Cluster 2 was characterized by *P. latifolius* and showed the lowest values for salinity, soil cations (Na^+, Mg^{2+}, K^+,

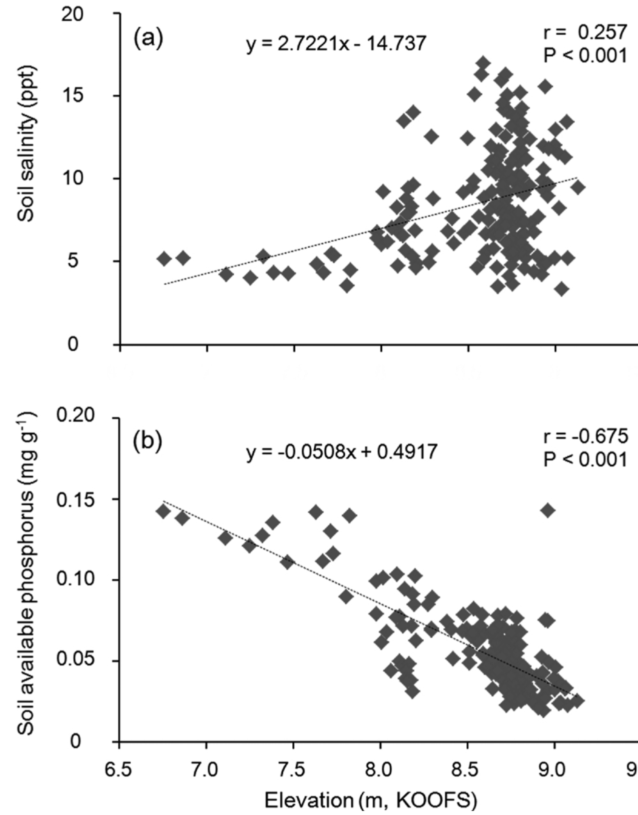

Fig. 3. Relationships between elevation and (a) soil salinity ($r = 0.257$, $P < 0.001$) and (b) soil available phosphorus ($r = -0.675$, $P < 0.001$) in the 203 sampling plots at Siheung Tidal Flat. Correlation between variables was assessed by Spearman's rank correlation (r). Elevation data from the Korea Ocean Observing and Forecasting System (KOOFS).

Table 2
Frequency of occurrence (%) and mean (standard error) coverage (%) of bare ground and salt marsh plants occurring at Siheung Tidal Flat (n = 203 plots).

	Frequency (%)	Coverage (SE) (%)
Bare ground	98	51.8 (3.9)
Suaeda japonica	41	22.4 (3.9)
Phacelurus latifolius	32	18.2 (3.8)
Carex scabrifolia	10	2.0 (0.9)
Suaeda glauca	5	2.6 (1.7)
Zoysia sinica	2	1.8 (1.5)
Phragmites australis	2	1.0 (1.0)
Artemisia fukudo	1	0.2 (0.2)

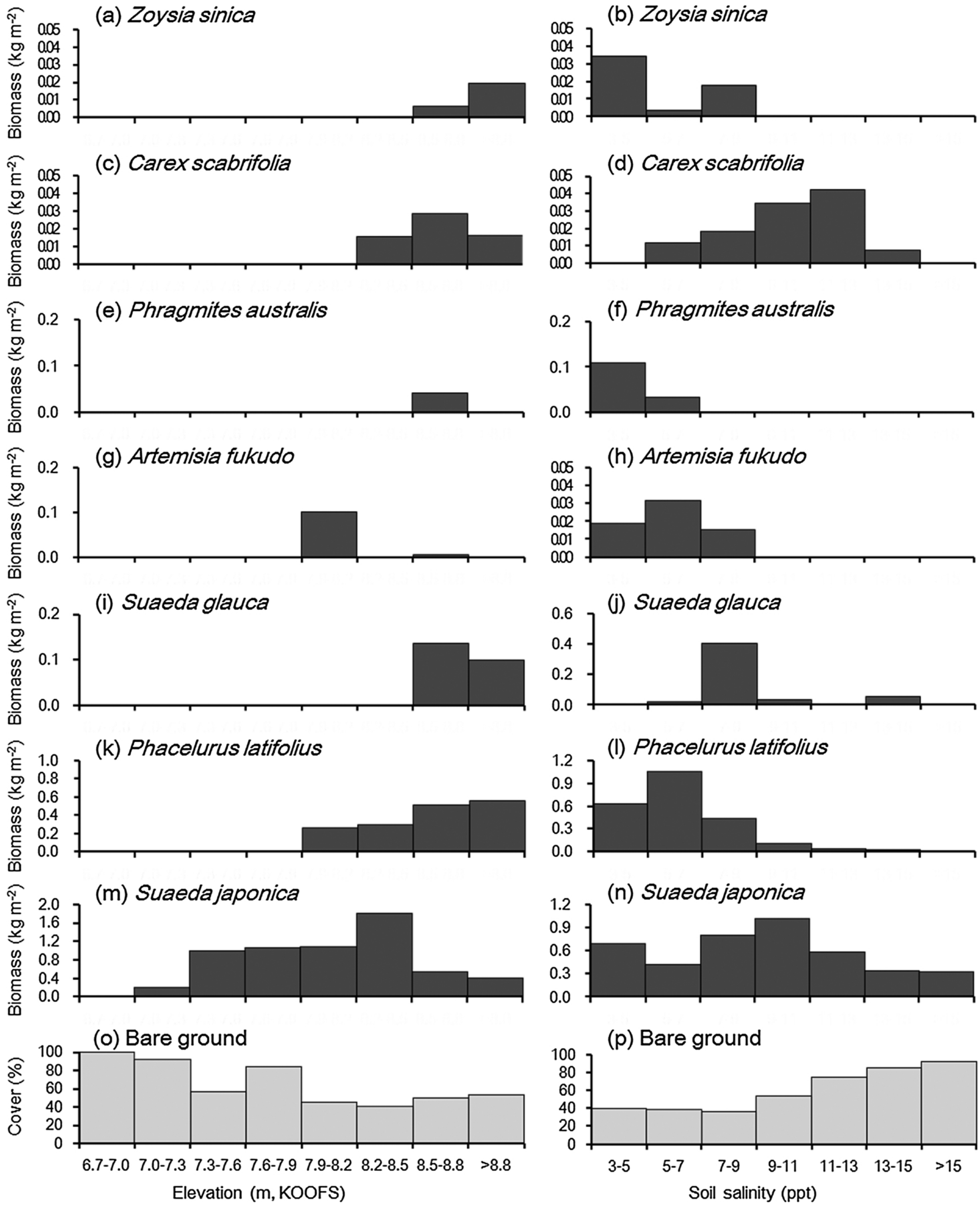

Fig. 4. Distribution of salt marsh plants (above-ground fresh biomass) and bare ground (cover) in relation to elevation and soil salinity in the 203 sampling plots at Siheung Tidal Flat. (a, b)*Zoysia sinica*, (c, d) *Carex scabrifolia*, (e, f) *Phragmites australis*, (g, h) *Artemisia fukudo*, (i, j) *Suaeda glauca*, (k, l) *Phacelurus latifolius*, (m, n) *Suaeda japonica*, (o, p) bare ground. Elevation data from the Korea Ocean Observing and Forecasting System (KOOFS). Above-ground fresh biomass and cover values are expressed as means. Black rectangles (■), salt marsh plants; grey rectangles (□), bare ground data.

Ca^{2+}), and available phosphorus ($P < 0.050$). *Carex scabrifolia* was the dominant species in Cluster 4, associated with the highest values for salinity and soil cations ($P < 0.050$). Cluster 1 was defined by high abundances of *S. glauca*, *Z. sinica*, *P. australis*, and *A. fukudo*, and by relatively low salinity compared with Cluster 4 ($P < 0.050$). Differences in plant community composition were also reflected in NMS (stress value = 3.4) (Fig. 6 and Table 4). Regarding plant species, each cluster is clearly separated. Plots in Cluster 2 were mostly located on the left of the ordination. They were low salinity, soil cations (Na^+, Mg^{2+}, K^+, Ca^{2+}), and available phosphorus. Also, species with a higher demand for flood frequency and salinity are more common in Cluster 3 on the upper part of the ordination.

Plant cover and biomass were positively correlated, but the linear relationship varied depending on plant species (Fig. 5). The positive correlation between plant cover and biomass was higher for *C. scabrifolia* ($r = 0.937$, $n = 83$, $P < 0.001$) than for *P. latifolius* ($r = 0.735$, $n = 64$, $P < 0.001$) or *S. japonica* ($r = 0.743$, $n = 83$, $P < 0.001$). *Suaeda japonica* showed a weak correlation with biomass at > 60% plant cover compared with *P. latifolius*.

Table 3
Mean values of environmental factors and salt marsh plant biomass across the four clusters. The values in parenthesis show the standard error. Different letters indicate significant differences in the factor between clusters based on the multiple comparison tests following the Kruskal-Wallis test ($P < 0.050$).

Variables	1	2	3	4
Elevation (m)	8.7 (0.03) ^{ab}	8.7 (0.03) ^{a}	8.5 (0.04) ^{b}	8.8 (0.04) ^{a}
Flood frequency (no. of days year^{-1})	70 (5) ^{ab}	74 (5) ^{b}	135 (11) ^{a}	67 (6) ^{b}
Soil water content (%)	29.8 (1.36)	29.3 (0.58)	32.4 (1.19)	28.6 (0.76)
Soil organic matter (%)	5.2 (0.36)	4.9 (0.11)	4.9 (0.12)	4.3 (0.18)
Soil pH	6.9 (0.11) ^{b}	6.8 (0.04) ^{b}	7.2 (0.04) ^{a}	7.4 (0.10) ^{a}
Soil salinity (ppt)	7.2 (0.72) ^{bc}	6.7 (0.26) ^{c}	8.9 (0.30) ^{ab}	10 (0.46) ^{a}
Soil Na^+ (mg g^{-1})	9.8 (1.07) ^{bc}	8.8 (0.36) ^{c}	12.2 (0.4) ^{ab}	14.1 (1.03) ^{a}
Soil Mg^{2+} (mg g^{-1})	2.1 (0.16) ^{b}	2.0 (0.05) ^{b}	2.6 (0.07) ^{a}	2.7 (0.15) ^{a}
Soil K^+ (mg g^{-1})	1.1 (0.05) ^{ab}	1.0 (0.02) ^{b}	1.1 (0.02) ^{a}	1.2 (0.05) ^{a}
Soil Ca^{2+} (mg g^{-1})	0.7 (0.06) ^{ab}	0.7 (0.02) ^{b}	0.8 (0.02) ^{a}	0.9 (0.06) ^{a}
Soil available phosphorus (mg g^{-1})	0.06 (0.007) ^{a}	0.04 (0.002) ^{b}	0.06 (0.003) ^{a}	0.05 (0.004) ^{a}
S. japonica (kg m^{-2})	0.19 (1.10) ^{b}	0 (0) ^{b}	1.62 (0.13) ^{a}	0 (0) ^{b}
P. latifolius (kg m^{-2})	0.08 (0.05) ^{b}	1.49 (0.09) ^{a}	0.01 (0.01) ^{b}	0 (0) ^{b}
C. scabrifolia (kg m^{-2})	0.01 (0.01) ^{b}	0 (0) ^{b}	0 (0) ^{b}	0.20 (0.02) ^{a}
S. glauca (kg m^{-2})	1.27 (0.45) ^{a}	0 (0) ^{b}	0 (0) ^{b}	0 (0) ^{b}
Z. sinica (kg m^{-2})	0.10 (0.05)	0 (0)	0 (0)	0 (0)
P. australis (kg m^{-2})	0.24 (0.15)	0.01 (0.01)	0 (0)	0 (0)
A. fukudo (kg m^{-2})	0.03 (0.03)	0 (0)	0.03 (0.02)	0 (0)

Table 4
Relationship between environmental factors and NMS ordination of the salt marsh plant community based on *envfit* (1000 permutations).

Factors	NMS1	NMS2	r^2	P
Elevation (m)	−0.39021	−0.92073	0.1698	0.001
Flood frequency (no. of days year^{-1})	0.38205	0.92414	0.1600	0.001
Soil water content (%)	0.18920	0.98194	0.0505	0.010
Soil organic matter (%)	−0.25882	0.96593	0.0141	0.312
Soil pH	0.98920	0.14657	0.1735	0.001
Soil salinity (ppt)	0.99990	0.01446	0.2128	0.001
Soil Na^+ (mg g^{-1})	0.99971	0.02393	0.2343	0.001
Soil Mg^{2+} (mg g^{-1})	0.98934	0.14565	0.2398	0.001
Soil K^+ (mg g^{-1})	0.99552	0.09458	0.2100	0.001
Soil Ca^{2+} (mg g^{-1})	0.99979	−0.02030	0.1550	0.001
Soil available phosphorus (mg g^{-1})	0.96545	0.26058	0.0945	0.001

4. Discussion

In salt marshes, halophyte zonation patterns are generally determined by environmental gradients (Ungar, 1998). At our Korean study site, each of seven salt marsh plant species had a distinct distribution range along gradients of elevation and salinity (Fig. 4). *Suaeda japonica* was the most dominant species and was found at a wide range of elevations; *P. latifolius* and *Z. sinica* were distributed further landward than other species; *C. scabrifolia* and *P. australis* were confined to higher-elevation plots; *A. fukudo* was mainly found at mid-range elevation plots. Thus, each salt marsh plant species had a different distribution range depending on the elevation and was likely influenced by different flood frequency ranges (Fig. 7). Bare ground coverage gradually increased with decreasing elevation because plants in low-elevation plots may not survive long periods of inundation (Dunton et al., 2001). The tidal pattern according to elevation is one of the most important factors determining the distribution of marsh plants (Adams, 1963; Congdon, 1981; Isacch et al., 2006; Hladik and Alber, 2014). Tidal flooding leads to decreased soil oxygen and results in anaerobic conditions (Ponnamperuma, 1984). The oxygen concentration in soil depends on the inundation time and flood frequency (Setter and Waters, 2003). When plants are completely submerged, decreased light, O_2, and CO_2 levels restrict photosynthesis (Colmer and Flowers, 2008). Plant growth is also restricted by characteristics of anoxic soil such as ion toxicity, ion transport interruption, and deficiencies in available minerals (Alhdad et al., 2015). Therefore, the elevation-related zonation pattern seems to reflect differences in the ability of each plant species to withstand flooding stress. In addition, most of the salt marsh

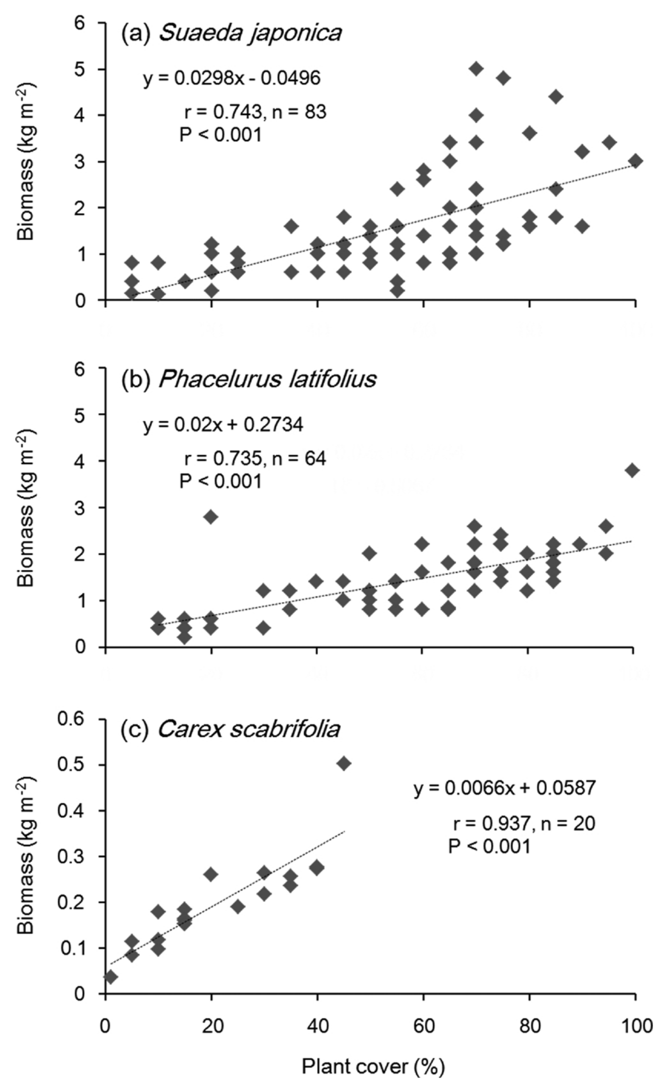

Fig. 5. The relationship between plant cover and biomass in (a) *Suaeda japonica*, (b) *Phacelurus latifolius*, and (c) *Carex scabrifolia*.

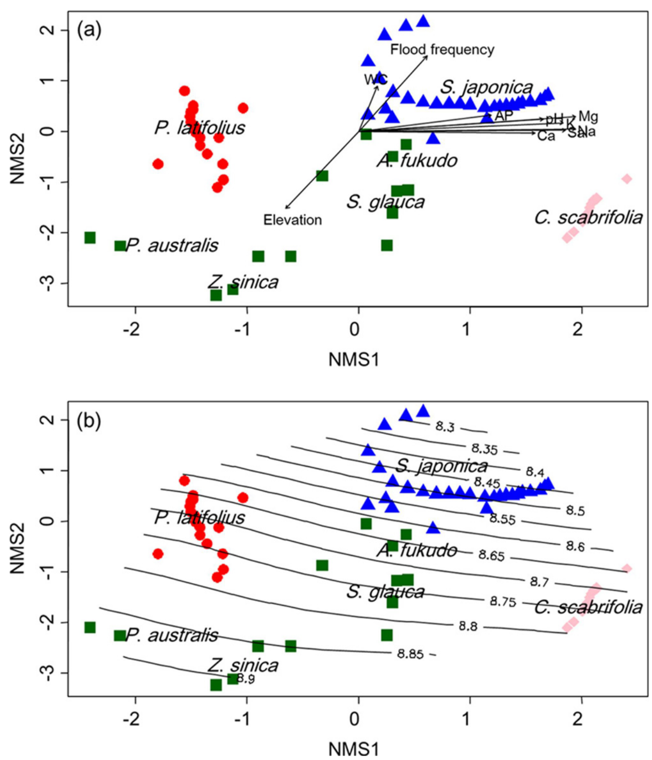

Fig. 6. NMS ordination based on the above-ground fresh biomass of salt marsh plant species at Siheung Tidal Flat. (a) Ordination with fitted vectors of environmental variables, (b) NMS ordination fitted by elevation. Seven salt marsh plants showed significant correlations with environmental factors ($P < 0.050$). Each symbol shape and color represents one of the four clusters (green: *A. fukudo*, *S. glauca*, *P. australis*, *Z. sinica*; red: *P. latifolius*; blue: *S. japonica*; pink: *C. scabrifolia*). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

plants are distributed at high elevation, which may indicate a realized niche reflecting potential interspecific competition in the upper intertidal zone.

Halophyte distribution is also related to salinity (Pennings et al., 2005). Although halophytes can tolerate some salt stress, individual species differ in their tolerance range (Flowers and Colmer, 2008). In contrast to its relationship with elevation, bare ground coverage tended to increase with increasing salinity. *Suaeda japonica* was common across the salinity range; *Z. sinica*, *P. australis*, *A. fukudo*, and *P. latifolius* were found at low salinities, whereas *S. glauca* and *C. scabrifolia* were found at mid-range salinities. Salt marsh plants can adapt to salt stress by regulating ion concentrations for water potential, regulating ion exchange, and accumulating ions. Their differential abilities may influence species distributions along the salinity gradient (Flowers and Colmer, 2008).

Salt marshes experience twice-daily flood and ebb tides, with daily variation in tidal height. The period of seawater immersion therefore depends on elevation. As elevation increases, the aerial exposure and drying times increase, leading to higher soil salinity (Pennings et al., 2005). At our study site, soil salinity did tend to increase with elevation, but with a wide range of variation in high-elevation plots (Fig. 3a). Most halophytes were found in high-elevation plots, and the extent of plant cover can influence soil water evaporation and hence soil salinity (Pennings and Bertness, 1999). In addition, irregular topography in the upper intertidal zone may affect soil salinity by determining the level of soil water saturation (De Rijk, 1995). Freshwater inflows from precipitation and rivers can also contribute to differences in salinity between bare grounds and plant-covered habitats (Horton and Murray, 2007). Soil available phosphorus tended to decrease as elevation increased (Fig. 3b). Higher flood frequencies at lower elevation may increase the supply of available phosphorus to plants through mineralization, whereas at higher elevation (lower flood frequency) increased desiccation can inhibit nutrient diffusion and mass flow (He and Dijkstra, 2014). Plant cover had a smaller effect on soil available phosphorus than on soil salinity (Fig. 3a and b), indicating that phosphorus concentration may be determined by sediment water content rather than by biological processes (Shao et al., 2013). Available phosphorus concentration can therefore be significantly affected by elevation.

Our results showed a high correlation between plant cover and biomass but with some differences among plant species (Fig. 5). In particular, the most abundant plant, *S. japonica*, showed considerable variability in the relationship between percentage cover and biomass. This variation may be driven by a combination of individual growth form, vegetation structure, habitat type, and environmental gradients (Jiang et al., 2017). At our study site, plant cover was recorded to the nearest 5% at each plot. A previous study showed that the sampling technique can increase the error for individual species (Hanley, 1978). However, plant biomass can also be quantitatively measured for small individual species using an electronic balance, which can provide ecologically important information about plant distribution and productivity (Jiang et al., 2017). Therefore, the biomass data collected in this study are a more objective index, and allowed a more rigorous statistical analysis because the error range between samples is smaller than for plant cover data.

The relationship between species distribution and environmental factors in this salt marsh is shown clearly by the results of CA and NMS analysis (Fig. 6 and Table 3). In particular, the distribution of seven salt marsh plants showed significant correlations with environmental factors ($P < 0.05$). *Suaeda japonica*, defining Cluster 3, was the dominant species at the lowest elevation and at the highest flood frequency and occurred across the range of soil salinities. These results are consistent with those of previous studies. *Suaeda japonica*, an annual plant that grows rapidly in its early stages, is widely distributed throughout salt marshes on the west coast of Korea (Lee and Ihm, 2004). The species copes with salt stress by means of increased levels of betaine and accumulation of glycinebetaine (Yokoishi and Tanimoto, 1994; Hayakawa and Agarie, 2010). These characteristics allow it to dominate in areas with wide ranges of immersion and salinity. Therefore, *Suaeda japonica*, the most dominant species in the study site, is also well-adapted to a high-salinity waterlogged environment. *Phacelurus latifolius*, the principal species in Cluster 2, dominated at mid-high elevations where soil salinity, cations (Na^+, Mg^{2+}, K^+, Ca^{2+}), and available phosphorus negatively affected distribution and productivity. Min (2015) showed that *P. latifolius* is a high-elevation marsh species. This plant is dominant in freshwater or brackish wetlands, where it is confined to the upper intertidal zone (Shim et al., 2009). Available phosphorus may also be reduced by the more prolonged drying of the soil at high elevation (He and Dijkstra, 2014). Elevation, salinity, cations, and available phosphorus may therefore determine the distribution of *P. latifolius*. *Carex scabrifolia*, in Cluster 4, was distributed at mid-high elevation and at the highest salinity and cation values in the study area. This species commonly occurs together with *P. australis* at high elevations in salt marshes (Chen et al., 2007; Zhou et al., 2007). In Japan, *C. scabrifolia* is typically found on sandbars in lagoons and estuaries (Hodoki et al., 2014), which may experience high salinities. In general, lagoons and the upper reaches of salt marshes may have some high-salinity microhabitats, and *C. scabrifolia* may prefer these areas because of reduced competition with other plant species. *Suaeda glauca*, *Z. sinica*, and *P. australis* defined Cluster 1, which was distributed at high elevation, whereas *A. fukudo* (Cluster 1) was found at mid-elevation areas in the study site. Salinity in Cluster 1 plots was relatively low compared with that in other cluster plots. *Phragmites australis* is widely distributed throughout freshwater, brackish, and salt marsh habitats, tolerating a wide range of salinities, but usually predominates in brackish wetlands. Its distribution is limited to salt marches with a high elevation

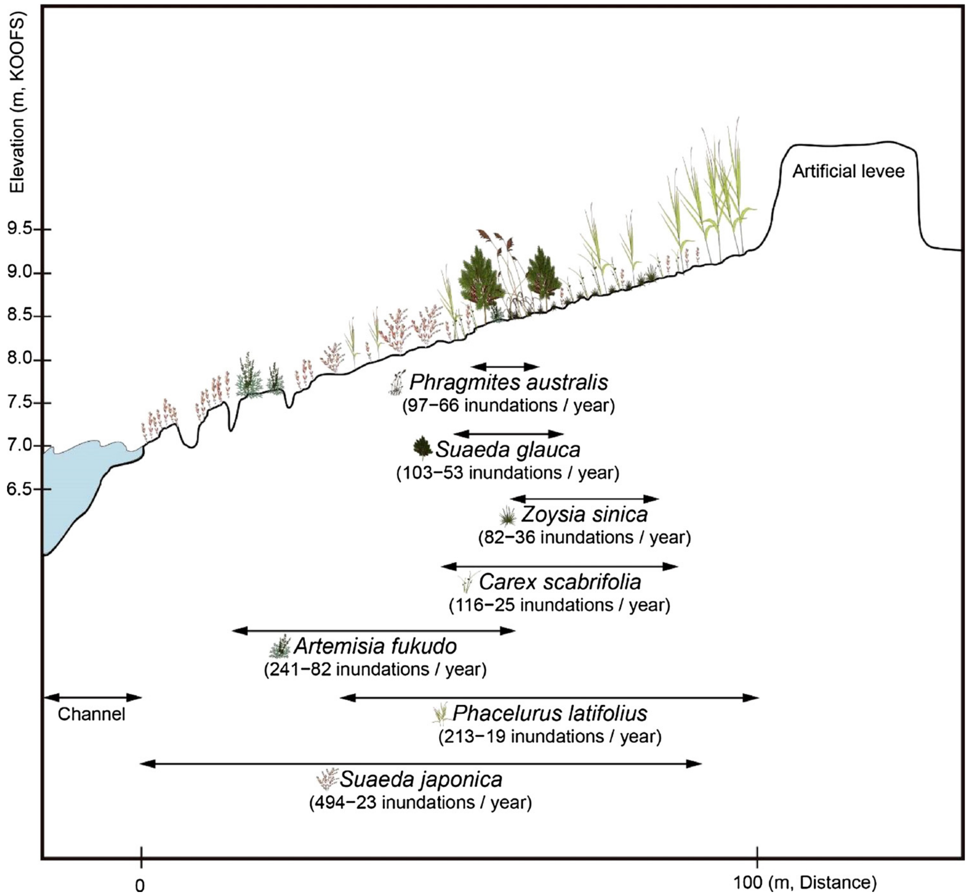

Fig. 7. Plant distribution and flood frequency in relation to elevation at Siheung Tidal Flat. Elevation data from the Korea Ocean Observing and Forecasting System (KOOFS).

(Chambers et al., 1999). At our study site, *Zoysia sinica*, a pioneer species on salt marsh mudflats (Kim et al., 1986), occurred in areas with high elevation and relatively low salinity. This is consistent with previous studies on this halophyte showing that it occurs in salt marshes on the convex surfaces of highly elevated regions (Min and Je, 2002), a pattern suggesting that it is vulnerable to flooding.

In conclusion, the seven halophyte species of Siheung Tidal Flat showed different distribution ranges and productivities in relation to elevation and salinity gradients. The high tidal range and the presence of salt marsh plants significantly increased environmental variability. Each species has individual tolerances and a preferred habitat along environmental gradients. Our study site may be used as a reference wetland for restoration of macrotidal salt marshes. Our quantitative field data provide valuable basic information for species selection and planting locations, which may promote plant establishment and improve survival rate in restored salt marshes.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.aquabot.2018.03.005.

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