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Differences in crab burrowing and halophyte growth by habitat types in a Korean salt marsh

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A R T I C L E I N F O

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A B S T R A C T

Crabs and halophytes are important indicators of soil composition and fertility in salt marsh ecosystems. Many previous studies have examined the effects of crab excavation on soil properties, but little is known about the combined effects of crabs and halophytes on salt marsh soils. The purpose of this study was to identify the distribution of halophytes and crabs in a macrotidal salt marsh, and to determine effects of the combination of crabs and halophytes on the physicochemical properties of soils. Vegetation structure and soil properties in relation to seed dispersion distance and habitat type were analyzed using Kruskal-Wallis tests, Cluster Analysis (CA), and Principal Component Analysis (PCA). Plant biomass and height of individual marsh plants tended to be higher at distances > 1 m from stands of parent plants. Crabs preferred habitats with high vegetation cover. Low densities of burrowing crabs and halophytes also caused considerable changes in soil properties. The combination of crabs and halophytes increased the spatial variability of physicochemical parameters in these salt marsh soils. Thus these combinations may be important to a complete understanding of plant distribution and soil nutrient cycling in salt marsh ecosystems.

1. Introduction

Burrowing animals play important roles in soil ecosystems as consumers, degraders, and habitat disturbers (Wang et al., 2010), exerting a significant influence on organic matter and nutrient dynamics (Hättenschwiler and Gasser, 2005). Crabs are one of the important constituents of salt marsh ecosystems and can have a significant impact on the salt marsh sedimentary environment (Smith et al., 1991). Their burrowing activity is a form of bioturbation (Meysman et al., 2006), which changes the structure of anoxic wetland soils, transports particulate matter and accelerates ecosystem nutrient cycling (Bertness, 1985; Warren and Underwood, 1986). Changes in the physicochemical composition of the soil as a result of crab burrowing can directly or indirectly affect the salt marsh plant community (Iribarne et al., 1997; Botto et al., 2006).

Plants can also have a significant impact on soil chemical processes by changing physical factors in the soil (Vitousek and Walker, 1989; Wedin and Tilman, 1990; Vinton and Burke, 1995). Individual plant species play an important role in determining soil fertility and have a direct positive feedback impact on soil nutrient cycling (Pastor et al., 1984; Berendse et al., 1987; Hobbie, 1992). Litter decomposition rate, which is affected by microenvironmental conditions such as pH, temperature, and other physical factors, drives changes in soil nutrient concentrations (Hector et al., 2000). The plant rhizosphere can also affect soil organic matter decomposition and nutrient dynamics (Hättenschwiler and Gasser, 2005). Also, plant density is affected by levels of disturbance and spatial heterogeneity in soils (Grace, 1999). For example, annual plants which scatter their seeds may show variation in the dispersal distance from individual parent plants. Variations in seed density according to distance from the parent plants may determine the degree of intraspecific competition for limited resources, and may have a considerable influence on plant growth (Weiner and Thomas, 1986).

In salt marshes, crabs can affect the structure and function of plant communities together with the soil environment (Wang et al., 2010; Martinetto et al., 2016). Crab burrowing disturbs anoxic soil, affecting its physical structure (Fanjul et al., 2007; Fanjul et al., 2008), nutrient cycling and energy flow (Montague, 1981; Botto et al., 2006), and the structure and productivity of mangrove forests (Smith, 1988; Smith et al., 1991). To date, most studies of these processes have been carried out in mangrove wetlands. Although there has been some researches into the structure and ecological characteristics of salt marshes (Ungar, 1998; Varty and Zedler, 2008; Davy et al., 2011), little is known of the interactions between plant communities and burrowing crabs, despite their potential importance to the functioning of salt marsh ecosystems.

The Siheung Tidal Flat is one of the large salt marshes in Korea and

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has a wide range of halophyte species distributed in relation to the tidal range (Bang et al., 2018). The burrowing crab *Helice tientsinensis* is common in the *Suaeda japonica* community, the dominant halophyte of the Siheung Tidal Flat. No study was conducted examining the role of crabs and halophytes in sedimentary characteristics of Korean salt marshes. Therefore, this study aimed to identify the distribution of the dominant crabs and halophytes on the Siheung Tidal Flat and determine effects of the combination of crabs and halophytes on the physico-chemical properties of soils. The specific questions were: (1) What determines the distribution of plant populations and community characteristics? (2) How does the presence of crab and plant affect soil characteristics?

2. Material and methods

2.1. Study site

The Siheung Tidal Flat, a macrotidal salt marsh, is one of the large tidal flats in Korea. Deep tidal channels are created by the high tidal range (from 4 to 9 m), and salt marsh plants are widely distributed in the intertidal zone (Wells et al., 1990). The government has recognized the ecological importance of this area, which has been designated as a Coastal Wetland Protected Area since 2012 (area ~0.71 km^2). This study was conducted in the upper intertidal zone of the Siheung Tidal Flat (37° 23′ 40.0″ N, 126° 46′ 13.6″ E), which has a relatively consistent elevation (8.7–8.8 m) and occupies a large proportion of the study area (Fig. 1). This area was formed by macro-tides and semidiurnal tides. The burrowing crab *Helice tientsinensis* Rathbun is mainly distributed in the upper intertidal zone of tidal flats on the west coast of Korea (Marine Arthropod Depository Bank of Korea, 2009). *Suaeda japonica* Makino is the dominant halophyte at the study site (Bang et al., 2018). This annual plant is patchily-distributed across the study area, with the patches separated by unvegetated mudflats. Flowers of *S. japonica* bloom from July to September, with seeds forming from October to November. Seeds dispersed from the parent plant each year begin to germinate in the spring of the following year. *Suaeda japonica* communities support dense populations of *Helice tientsinensis*, the most abundant burrowing crab species in this salt marsh. Densities are estimated as 8–48 individuals/m^2. The crab burrows are easily identified in the *S. japonica* community and also occur in areas with little or no vegetation cover. The fiddler crab *Uca arcuata* De Haan is mainly observed in the unvegetated low intertidal zone, which was excluded from the study area.

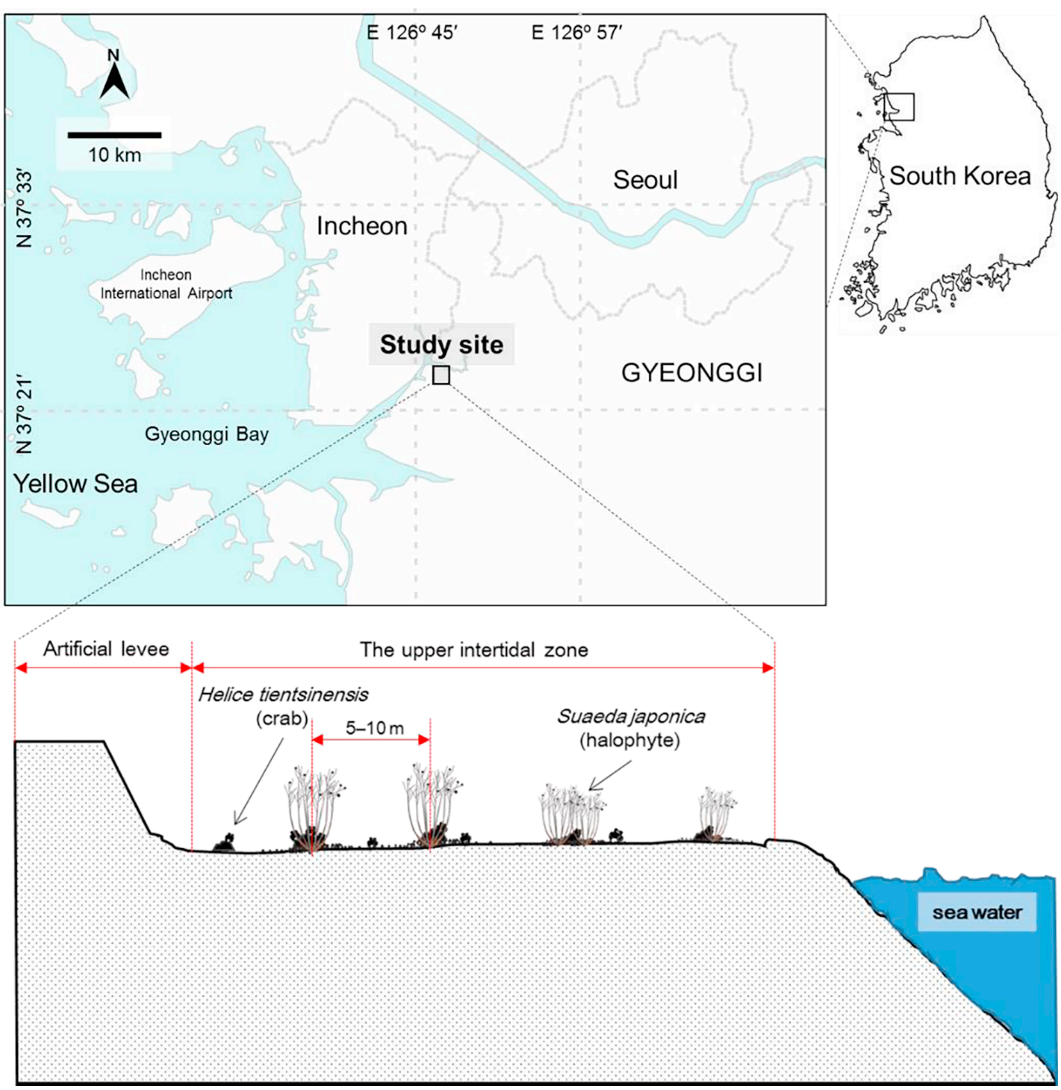

Fig. 1. The location of the study site and cross-section of the study site showing the distribution of the dominant crabs and halophytes.

The study area is located in the mid-latitude temperate climatic zone. The annual precipitation in 2014 was 788.1 mm, with > 56% of the rain falling between July and September. The mean annual temperature in 2014 was 12.8 °C (Korea Meteorological Administration, http://www.kma.go.kr/). The mean height above sea level is 8.8 m and the area is irregularly submerged (1–12 times per month).

2.2. Field survey

The first field survey investigated the growth of *S. japonica* and soil properties according to the distance of seed dispersal from the parent plants, which are dead plants from the previous year. These dead plants occur in patches with a diameter of ~50 cm. In salt marsh plants of the Family Chenopodiaceae, most seeds disperse < 1 m from the parent plants, but tidal movement can scatter seeds at low density over distances > 1 m (Ellison, 1987). Based on these patterns, three zones were defined in relation to distance from parent plants of *S. japonica*: a Center zone (0 m) at the location of the parent plants; a Near zone, within 1 m radius of them; and a Remote zone covering the area > 1 m (range 2–5 m, similar patchy distribution) distant from the parent plants. Ten replicate permanent plots (0.5 × 0.5 m) were randomly established in each zone (Center, Near, Remote). The vegetation survey was conducted every 2 months from April to October 2014. In each plot, the number of stems and plant height were measured and above-ground dry weight biomass was measured in October 2014. Soil samples were taken during the lowest tidal periods of October 2014 to eliminate the effects of tides and precipitation on each plot. Soil samples were taken from three random subsamples at 5 cm depth in each plot using a soil corer (Eijkelkamp BV, Netherlands). The three subsamples representing each plot were mixed thoroughly (~300 ml volume per sample) and stored at 4 °C in a sealed plastic bag until soil analysis was performed.

To investigate the second field survey, we identified the distribution pattern of the dominant crabs and halophytes in the study area. Recent studies have shown that burrowing crabs preferred well-vegetated habitats to reduce hazards from drying and predators (He and Cui, 2015; Chen et al., 2016). At the study site, the burrow density was higher in the vegetated habitats than in bare ground. Also, the burrow density was higher at high plant coverage than at low plant coverage (Fig. A.1). Each plant is affected by crabs in the study site. There were no habitats where the plants were living alone. To measure their relative effects, four habitat types were defined in the study area according to the densities of burrowing crabs (BC) and plants (P) (Table 1): the 'Control' habitat consisted of a mudflat lacking both crab burrows and plants; the 'Low BC' habitat lacked vegetation and had soil disturbed by a low density of burrowing crabs (2–3 burrows); the 'Low BC + P' habitat had a low density of burrowing crabs (degree of soil disturbance was similar to Low BC, 2–4 burrows) and a sparse cover of *S. japonica* (1–2 individuals); the 'High BC + P' habitat had higher densities of both crabs (8–12 burrows) and *S. japonica* (4–9 individuals). Each habitat type was randomly distributed throughout the salt marsh. Ten replicate plots (0.5 × 0.5 m) were randomly established in each habitat (Control, Low BC, Low BC + P, High BC + P). To avoid spatial autocorrelation (Schlesinger et al., 1996), each plot was installed > 5 m away from any neighboring plots. A vegetation survey and soil sampling was conducted in each plot in October 2014. The vegetation survey measured plant density, height, and coverage. Percentage cover was recorded to the nearest 5%. Soil samples were collected simultaneously in the same manner as in the first field survey. To estimate burrowing crab density in the study area, numbers of burrows in each treatment plot were counted in October 2014.

Table 1
Habitat types defined according to crab and plant abundance on Siheung Tidal Flat, Korea.

Habitat type	No. burrows (no./ 0.25 m^2)	No. plants (no./ 0.25 m^2)	Plant height (cm)	Plant coverage (%)	Material composition
Control					Mudflat
Low BC	2–3				Mudflat, crabs
Low BC + P	2–4	1–2	52–59	15–35	Crabs, plants
High BC + P	8–12	4–9	59–73	70–90	Crabs, plants

Low BC: low density of crab burrows; Low BC + P: low density of both crab burrows (Low BC) and plants (P); High BC + P: higher densities of both crab burrows (High BC) and plants (P).

2.3. Soil analysis

Soil water content (WC) was measured by weight loss after drying at 105 °C for 48 h. Soil organic matter (OM) content was determined by loss-on-ignition (combustion at 550 °C for 4 h) (John, 2004). WC and OM are the physical properties of soil, and other soil factors are the chemical properties of soil. To measure soil pH and electrical conductivity (EC), the soil samples were dried naturally in the shade for 2 weeks and then the soil was passed through a 2 mm sieve; next, the soil was mixed in distilled water (1:5) for 1 h, and pH and EC were measured using a multiparameter bench meter (PC2700, Eutech, Singapore). Soil carbon (C) and nitrogen (N) content was measured using an elemental analyzer (Flash EA 1112, Thermo Electron Corporation, USA). Available phosphorus (AP) and cations (Na^{+}, Mg^{2+}, K^{+}, Ca^{2+}, Fe^{2+}), were extracted by the Mehlich-3 extraction method (Ziadi and Tran, 2007). The ferric ion in the soil is one of the variables indicating the redox potential state (Takai and Kamura, 1966). This ion can exist in the form of oxidized iron in a marshy soil layer with reduced oxygen (Kristensen, 2000). AP was measured by colorimetry (Ziadi and Tran, 2007) and cations measured using an Inductively Coupled Plasma Emission Spectrometer (ICP-730ES, Varian, Australia).

2.4. Data analysis

All data were analyzed using R software version 3.3.3. (R Core Team, 2017). Nonparametric statistics were used because the variables were not normally-distributed and the number of samples was small. Kruskal-Wallis tests were used to compare plant growth or soil properties in relation to distance from the parent plants. Kruskal-Wallis tests were also used to compare soil properties in the different habitat types defined by crab burrow density and vegetation cover. Multiple comparison tests were performed using the *kruskalmc* function in the 'pgirmess' package within the R program if there were significant differences in the Kruskal-Wallis test ($P < 0.05$). For Cluster Analysis using Ward's method, the sampling plots defined in relation to distance from parent plants were classified into two groups, and the sampling plots in different habitat types were classified into four groups using the hclust function (raw data) within the R program. Principal Component Analysis was used to investigate the relationship between soil properties and sampling plots (seed dispersal distances, habitat types). PCA was performed using a correlation matrix of 12 soil variables, with the variables standardized before analysis to compensate for different scales.

3. Results

3.1. Vegetation survey

The number of *S. japonica* stems decreased over time, with the pattern of change varying with distance from the parent plants (Fig. 2a). Stem density decreased most rapidly in the Center zone from April to June. After June, the rate of decline was very similar in the Center and Near zones. At each time point, the Remote zone had the lowest number of *S. japonica* stems. The mean density of stems was significantly different in October (x^2 = 25.39, d.f. = 2, P < 0.001), with final values of 34.0 ± 1.05 stems 0.25 m^{-2} (Near zone), 24.0 ± 1.34 stems 0.25 m^{-2} (Center zone), and 5.4 ± 0.62 stems 0.25 m^{-2} (Remote zone).

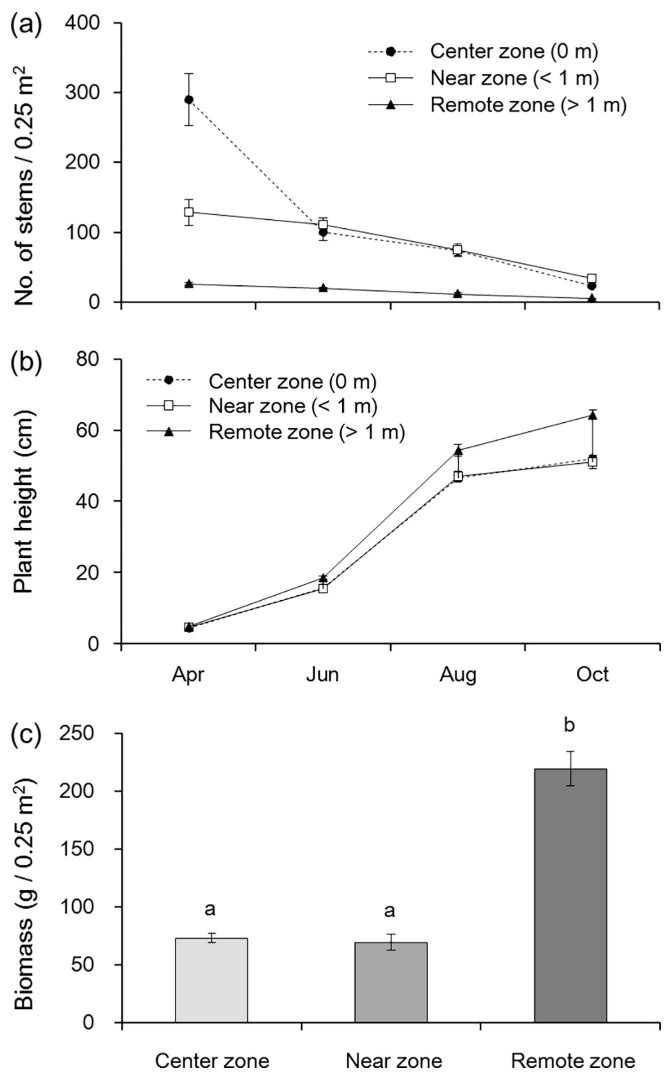

Fig. 2. (a) Number of stems, (b) plant height, and (c) above-ground biomass of *Suaeda japonica* in three zones defined with respect to distance from parent plants. Different lower-case letters above the bars in (c) indicate significant (P < 0.05) differences between zones in multiple comparisons following the Kruskal-Wallis test. Each error bar represents the standard error (n = 10).

The height of the *S. japonica* plants was inversely related to distance from the parent plants, with highest values in the Remote zone (Fig. 2b). The effect of distance on plant height was greatest in October (x^2 = 19.36, d.f. = 2, P < 0.001). Mean height was very similar in the Near (51.06 ± 1.85 cm) and Center zones (52.08 ± 0.86 cm), but was significantly greater (P < 0.05) in the Remote zone (64.38 ± 1.33 cm).

Above-ground biomass also differed significantly (x^2 = 19.73, d.f. = 2, P < 0.001) with distance from parent plants (Fig. 2c). Biomass was nearly three times greater (P < 0.05) in the Remote zone (219.27 ± 14.99 g 0.25 m^{-2}) than in the Near (69.43 ± 6.88 g 0.25 m^{-2}) and Center zones (72.86 ± 4.05 g 0.25 m^{-2}).

3.2. The effect of plant density on soil properties

Physical and chemical properties of the soil varied depending on plant density. There was little difference between the Center and Near zones, but several soil parameters in Remote zone were significantly different: WC (x^2 = 15.35, d.f. = 2, P < 0.001), OM (x^2 = 15.58, d.f. = 2, P < 0.001), C (x^2 = 14.00, d.f. = 2, P < 0.001), AP (x^2 = 15.80, d.f. = 2, P < 0.001), and K^+ (x^2 = 9.01, d.f. = 2, P < 0.05) (Table 2). Specifically, the Remote zone showed significantly higher values for WC, OM, C and K^+ and significantly lower AP than the Center and Near zones (P < 0.05).

Table 2
Mean (± SE) values for soil properties in three zones defined with respect to distance from parent plants of *Suaeda japonica*.

Soil properties	Center zone (Mean ± SE)	Near zone (Mean ± SE)	Remote zone (Mean ± SE)
Water Content (%)	30.9 ± 0.38^{a}	31.6 ± 0.41^{a}	33.8 ± 0.52^{b}
Organic Matter (%)	3.32 ± 0.07^{a}	3.41 ± 0.10^{a}	3.97 ± 0.12^{b}
pH	5.96 ± 0.01^{a}	6.03 ± 0.02^{ab}	6.09 ± 0.03^{b}
Electric Conductivity (mS/cm)	10.38 ± 0.51	10.96 ± 0.53	10.73 ± 0.44
Carbon (%)	29.21 ± 2.80^{a}	25.03 ± 1.34^{a}	38.08 ± 3.07^{b}
Nitrogen (%)	9.82 ± 0.18	9.83 ± 0.17	10.92 ± 0.42
Available Phosphorus (mg/kg)	20.71 ± 0.91^{b}	19.44 ± 1.23^{b}	11.42 ± 1.40^{a}
K^+ (mg/g)	0.65 ± 0.03^{a}	0.65 ± 0.02^{a}	0.79 ± 0.04^{b}
Ca^{2+} (mg/g)	0.43 ± 0.03^{ab}	0.39 ± 0.01^{a}	0.50 ± 0.02^{b}
Na^+ (mg/g)	8.13 ± 0.54	8.48 ± 0.46	8.03 ± 0.37
Mg^{2+} (mg/g)	1.85 ± 0.12	2.08 ± 0.11	2.12 ± 0.12
Fe^{2+} (mg/g)	0.24 ± 0.01^{b}	0.20 ± 0.01^{a}	0.25 ± 0.03^{ab}

Different superscript letters indicate significant differences between the means based on multiple comparisons following the Kruskal-Wallis test (P < 0.05).

Two groups of plots were identified by CA according to distance from parent plants (Fig. A.2). Group A contained plots from the Center and Near zones, whereas Group B consisted mainly of Remote zone plots plus two plots from the Center zone. Principal Component Analysis indicated two groups of soil properties according to the distance from the parent plants (Fig. 3). On the left side of the graph, the plots of the Center zone and the Near zone overlap; most of the plots in the Remote zone are towards the right side of the graph. The first component (PC1) explained 50.66% of the data variance (Table 3). PC1 loaded positively from OM, pH, C, N, K^+, and Ca, and negatively from AP. The second component (PC2) explained 21.53% of the data variance. PC2 loaded negatively from EC, Na^+, and Mg^{2+}, and positively from WC, pH, C, and N.

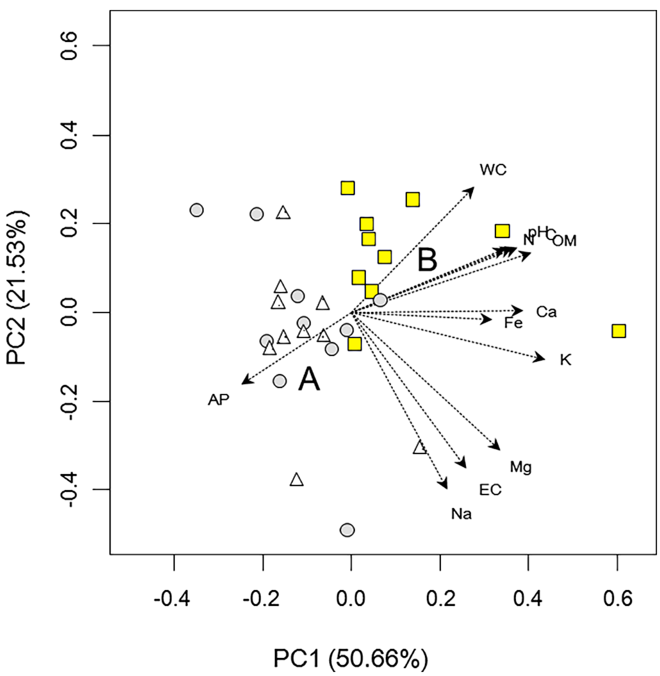

Fig. 3. Principal Component Analysis of soil properties for seed dispersion distances in the sampling plots on Siheung Tidal Flat. Seed dispersion distances: A, Center (○) and Near (△), B, Remote (□); WC, water content; OM, organic matter; EC, electrical conductivity; AP, available phosphorus.

Table 3
PCA loadings and explained variance for soil properties between seed dispersion distances on Siheung Tidal Flat. The values are the eigenvectors of the first three PCs.

Soil factors	PC1	PC2	PC3
Water Content	0.238	0.370	0.310
Organic Matter	0.348	0.178	0.052
pH	0.311	0.191	0.297
Electric Conductivity	0.221	−0.465	0.142
Carbon	0.322	0.190	−0.489
Nitrogen	0.299	0.185	−0.428
Available Phosphorus	−0.214	−0.215	−0.509
K^+	0.183	−0.524	0.004
Ca^{2+}	0.287	−0.409	0.146
Na^+	0.372	−0.139	−0.104
Mg^{2+}	0.331	0.005	−0.245
Fe^{2+}	0.272	−0.023	0.139
% of Variance	50.660	21.530	6.578
Cumulative %	50.660	72.190	78.766

3.3. Soil properties by habitat type

Physicochemical parameters of the soil also varied in relation to crab burrow density and the structure of the *S. japonica* community (plant density, height, and coverage), as shown by significant differences among habitat types (d.f. = 3, $P < 0.001$) (Table 4). The presence of burrowing crabs (Low BC) was associated with significantly higher values for OM, EC, Ca^{2+}, Na^+ and Mg^{2+}, and significantly lower pH and Fe^{2+} compared to the Control habitat ($P < 0.05$). Soil WC, pH, C and N tended to be higher in the presence of *S. japonica* (Low BC + P, High BC + P), whereas EC, AP, K^+, Ca^{2+}, Na^+, and Mg^{2+} tended to decrease with increasing plant density compared to the Low BC habitat. Values of WC, OM, C and N were significantly higher, and AP and Fe^{2+} concentrations significantly lower, in the High BC + P habitat compared to the Control habitat ($P < 0.05$).

Table 4
Mean (± SE) values for soil properties in four defined habitat types on Siheung Tidal Flat.

Soil Properties	Control (Mean ± SE)	Low BC (Mean ± SE)	Low BC + P (Mean ± SE)	High BC + P (Mean ± SE)
Water Content (%)	27.58 ± 0.35^{a}	30.38 ± 0.56^{ab}	31.59 ± 0.63^{bc}	33.8 ± 0.52^{c}
Organic Matter (%)	3.03 ± 0.08^{a}	3.81 ± 0.09^{b}	4.06 ± 0.12^{b}	3.97 ± 0.12^{b}
pH	6.04 ± 0.01^{bc}	5.94 ± 0.02^{a}	5.97 ± 0.02^{ab}	6.09 ± 0.03^{c}
Electric Conductivity (mS/cm)	12.5 ± 0.24^{ab}	17.3 ± 0.40^{c}	15.0 ± 0.59^{bc}	10.7 ± 0.44^{a}
Carbon (%)	14.06 ± 0.64^{a}	22.34 ± 0.49^{ab}	28.93 ± 1.26^{bc}	38.08 ± 3.07^{c}
Nitrogen (%)	8.83 ± 0.11^{a}	9.22 ± 0.11^{ab}	10.1 ± 0.18^{bc}	10.92 ± 0.42^{c}
Available Phosphorus (mg/kg)	28.1 ± 1.82^{bc}	32.9 ± 1.73^{c}	19.9 ± 2.42^{ab}	11.4 ± 1.40^{a}
K^+ (mg/g)	0.85 ± 0.02^{ab}	1.14 ± 0.03^{bc}	1.03 ± 0.04^{b}	0.79 ± 0.04^{a}
Ca^{2+} (mg/g)	0.32 ± 0.03^{a}	0.71 ± 0.02^{c}	0.68 ± 0.02^{bc}	0.50 ± 0.02^{ab}
Na^+ (mg/g)	9.54 ± 0.38^{ab}	12.69 ± 0.32^{c}	10.81 ± 0.64^{bc}	8.03 ± 0.37^{a}
Mg^{2+} (mg/g)	2.58 ± 0.10^{ab}	3.74 ± 0.15^{c}	3.07 ± 0.20^{bc}	2.12 ± 0.12^{a}
Fe^{2+} (mg/g)	0.54 ± 0.05^{b}	0.33 ± 0.01^{a}	0.32 ± 0.02^{a}	0.25 ± 0.03^{a}

Different superscript letters indicate significant differences between the means based on multiple comparisons following the Kruskal-Wallis test ($P < 0.05$).
Low BC: low density of crab burrows; Low BC + P: low density of both crab burrows (Low BC) and plants (P); High BC + P: higher densities of both crab burrows (High BC) and plants (P).

The Cluster Analysis by habitat identified four groups of plots (Fig. A.3). Group A represented the mudflat with no crab burrows or vegetation (Control habitat). Group B consisted mostly of plots from the unvegetated burrowing crab habitat (Low BC) but also included some plots from the Low BC + P habitat. Group C contained most of the Low BC + P habitat plots (low crab burrow density, low density vegetation). Group D represented the High BC + P habitat, defined by the highest densities of crab burrows and vegetation. In addition, PCA revealed a clear separation between the soil properties of the four habitats (Fig. 4). The first component (PC1) explained 43.06% of the data variance (Table 5). Groups B and D were clearly separated along the PC1 axis, but there was some overlap between sampling plots in Groups B and C. PC1 loaded negatively from EC, AP, Na^+, Mg^{2+}, and K^+, and positively from WC, pH, C, and N. The second component (PC2) explained 33.28% of the data variance. The Control habitat (Group A) was clearly separated from the other three groups by PC2. PC2 loaded negatively from WC, OM, C, N, and K^+, and positively from Fe^{2+} and AP.

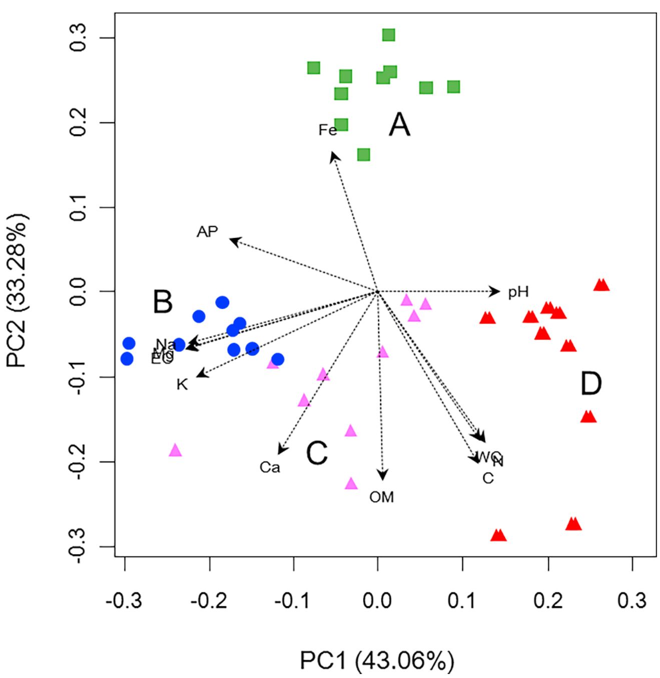

Fig. 4. Principal Component Analysis of soil properties for habitat types in the sampling plots on Siheung Tidal Flat. Habitat types: A, Control (■); B, Low BC (●); C, Low BC + P (▲); D, High BC + P (▲). WC, water content; OM, organic matter; EC, electrical conductivity; AP, available phosphorus.

Table 5
PCA loadings and explained variance for soil properties between habitat types on Siheung Tidal Flat. The values are the eigenvectors of the first three PCs.

Soil factors	PC1	PC2	PC3
Water Content	0.213	−0.357	−0.222
Organic Matter	0.008	−0.450	0.069
pH	0.256	0.000	0.706
Electric Conductivity	−0.410	−0.138	0.039
Carbon	0.209	−0.408	0.200
Nitrogen	0.225	−0.360	0.215
Available Phosphorus	−0.316	0.129	−0.057
K^+	−0.403	−0.123	0.104
Ca^{2+}	−0.406	−0.133	0.175
Na^+	−0.382	−0.203	0.205
Mg^{2+}	−0.212	−0.387	−0.070
Fe^{2+}	−0.097	0.338	0.517
% of Variance	43.060	33.280	9.148
Cumulative %	43.060	76.340	85.489

4. Discussion

This study provides new insights into how the dominant halophyte and crab species affect the biogeochemical properties of soil in a Korean macrotidal salt marsh. In contrast to previous studies (Botto et al., 2005; Escapa et al., 2008), we were able to distinguish the relative effects of plants and crabs on soil characteristics. Data on these biological factors are essential for understanding nutrient cycling and energy flow in salt marsh ecosystems.

Soil nutrient concentrations in salt marshes is influenced by various biological factors (Vernberg, 1993), including the growth of wetland plants. The growth characteristics (height and biomass) of *S. japonica* in the study area were significantly affected by the plant density in the study area (Fig. 2). The stem density of the early *S. japonica* increased with decreasing distance from the parent plants. Our results are consistent with those of Ellison (1987), and suggest quite limited seed dispersal in this species, with most seeds spread within 1 m from the parent plants. Tidal movements can transport seeds of *S. japonica* further from the parent plants (Huiskes et al., 1995; Min, 2005), but most seeds settle within 1 m (our Center and Near zones) during the low tide, and only a small number would have reached our Remote zone by soft tide during the high tide. Seeds of *S. japonica* may also be moved by rain. The extent of seed transport by these mechanisms will probably determine the seedling density of *S. japonica* throughout the salt marsh. In our study area, over time, the density of *S. japonica* stems decreased sharply in the Center and Near zones, so that at the end of the growing season stem density and height were similar in the two zones. This is probably due to increased intraspecific competition for limited resources and adjustment of stem densities by self-thinning (Yu et al., 2014). On the other hand, growth (biomass and height) of *S. japonica* was considerably higher in the Remote zone where density was relatively low. These individual plants experienced lower levels of intraspecific competition, and seem to have used more soil nutrients for growth than those in the Center and Near zones (Ellison, 1987; Cabaço et al., 2013).

In addition to significant differences in plant height and biomass with the change in stem density of *S. japonica*, the plant density was also associated with significant changes in soil properties (Table 2). In the CA and PCA results, plots from the Center and the Near zones (within 1 m from parent plants) formed a group showing similar soil properties. Remote zone plots were mostly separate from this first group but with some overlap (Figs. 3 and A.2). Halophytes in salt marshes play an important role in soil nutrient cycling (Sollie and Verhoeven, 2008). They can increase the concentrations of carbon and nitrogen in salt marsh soil (Sousa et al., 2010). Halophytes also play a role in maintaining and accumulating P in biomass (Sekiranda and Kiwanuka, 1997). In our study area, soil properties in the Remote zone were significantly different from those in the Center and Near zones. The higher WC in Remote zone plots may be a function of higher plant biomass, which reduces soil water evaporation (Pennings and Bertness, 1999). The highest contents of OM, C, N, K^+, Ca^{2+}, and Mg^{2+} were found in the high-biomass Remote zone, whereas AP content was lowest in this zone. This pattern suggests that differences in the growth of the halophyte depending on distance from the parent plants can affect soil organic content and therefore the C, N, P, and cation concentrations of the soil.

Suaeda japonica and the burrowing crab *Helice tientsinensis* are the dominant species in the study area and occupy similar habitats. In this salt marsh, the relationship between the habitat type and soil characteristics is shown clearly by the results of CA and PCA (Figs. 4 and A.3). In particular, there were significant differences in soil characteristics depending on habitat type (Table 4). The Control habitat without vegetation or burrowing crabs (Group A) was clearly differentiated from the other habitats. Tidal flat soils are strongly influenced by oxygen supply and the rate of OM decomposition, with a clear vertical zonation according to redox conditions. A near-surface ‘oxic’ zone is determined by the depth of oxygen penetration into the sediment; below this, a ‘suboxic’ zone contains nitrate, oxidized manganese and iron; the deepest ‘reduced’ zone is dominated by sulfate (Kristensen, 2000). In the study area, the Control habitat, consisting of bare ground without bioturbation, showed relatively low values of WC, OM, C, and N, while values for Fe^{2+} were relatively high compared to other habitats.

The habitat with soil disturbed by burrowing crabs (Group B, Low BC) was clearly separated from other habitats. Gutiérrez et al. (2006) reported that soil disturbed by crabs accounts for 23% to 58% of salt marsh surface area. This pattern results from the mixing of surface and deep soil by the burrowing crabs (McCraith et al., 2003), an activity that changes the microtopography of the soil surface by forming mounds (Warren and Underwood, 1986). By allowing oxygen to penetrate anoxic soils and increasing the transport of particulate matter, crab burrowing modifies the physicochemical properties and redox potential of soil (Fanjul et al., 2007). In our study area, WC, OM, C, and N were higher in the Low BC habitat compared to the Control habitat. This contrast may be a result of burrowing by the crabs. Crab burrowing activity can increase the surface area and create more interstitial spaces in which moisture is retained (Koo et al., 2007). The feeding activity of crabs can increase organic matter, C, and N contents (Botto et al., 2006; Gutiérrez et al., 2006). The presence of crabs causes the release of fecal pellets into the sediment leading to increase of organic matter (Casariego et al., 2011). Burrowing activity accelerates the mineralization of decomposing OM (Otani et al., 2010) and increases release of inorganic nutrients in forms available as nutrients for plants (Takeda and Kurihara, 1987; Mayer et al., 1995; Fanjul et al., 2007). In our study area, AP, K^+, Ca^{2+}, Na^+, and Mg^{2+} tended to be higher in areas excavated by crabs, but values of Fe^{2+} were lower than in the Control habitat. This may be the result of the excavation of the crabs changing the vertically compartmentalized anaerobic soil layer to aerobic soil (Kristensen, 2000).

Plots in Group C (Low BC + P) were similar to Group B (Low BC) in degree of crab disturbance, but differed in supporting a low density (1–2 individuals) of plants. These two groups therefore allowed us to measure the effects of low density vegetation on soil characteristics in crab-disturbed soil. In Principal Component Analysis, Groups B and C were separated, but with some overlap. In particular, the Low BC + P habitat showed higher values for WC, OM, C, and N content than the Low BC habitat. These results suggest that the emergence of plants in crab-disturbed soil may promote water retention by increasing the surface area of salt marsh soil (Botto and Iribarne, 2000; Li et al., 2017). Shading by plants may affect evapotranspiration in strong sunlight and the relatively high water content would then reduce the EC value (Pennings and Bertness, 1999). In addition, increased exudates from leaves and roots may have contributed to increased OM, C, and N content (Davis and Van der Valk, 1983; Neira et al., 2006). In our study area, cations (Na+, Mg^{2+}, K^+, and Ca^{2+}) and AP concentrations were highest in soil disturbed by crabs (Low BC), but decreased with the emergence of plants. This pattern suggests that these nutrients may be used for plant growth.

Group D (High BC + P) is a habitat with a high density of both burrowing carbs and plants. In our study area, crab burrows tended to be more numerous where vegetation was denser than in the Low BC + P habitat (Table 1). These results indicate that crabs may prefer a relatively well-vegetated habitat. Recent studies have shown that salt marsh vegetation may be a favorable habitat for crabs because it provides shelter from both dessication and from predators, and the plants themselves can be used as a food source (He and Cui, 2015; Chen et al., 2016). Also, soil disturbed by crabs can facilitate plant growth (Smith et al., 1991). Principal Component Analysis showed that Group D was clearly distinguished from Group A (without soil disturbance) and also from Groups B and C (with low soil disturbance by crab or crab + plant). These results indicate that the combination of crab burrowing and the growth pattern of *S. japonica* can have a significant impact on soil properties in the study area. In particular, Groups C and D showed similar patterns, but the highest values for WC, C, and N content were found in Group D (High BC + P). High densities of crab burrows and plants increased salt marsh soil disturbance. Consequently, water content would have increased due to plant shading and increased soil surface area (Botto and Iribarne, 2000; Li et al., 2017). In addition, high plant productivity (Montemayor et al., 2014), burrowing activity, and feeding behavior (Martinetto et al., 2016) may have contributed to the high C and N contents. On the other hand, cations and AP concentrations were lowest in the High BC + P habitat. This is probably due to the uptake of nutrients by the high density of growing vegetation.

The plant density is determined by the distance from the parent plants. The plant density is controlled by self-thinning in the center and near zones. Plant growth was affected by the plant density, and the biomass was low in these zones. In the remote zone, the plant density was relatively low, and the biomass was high. In addition, crab bioturbation is influenced by plant coverage (Fig. 5). Plant coverage was relatively high in the center, near and remote zones (similar coverage). Crabs affect the soil nutrients through active bioturbation at high plant coverages and thereby facilitate plant growth. The intensity of bioturbation was relatively low in areas with a low plant coverage (Low BC + P) or no vegetation (Control, Low BC).

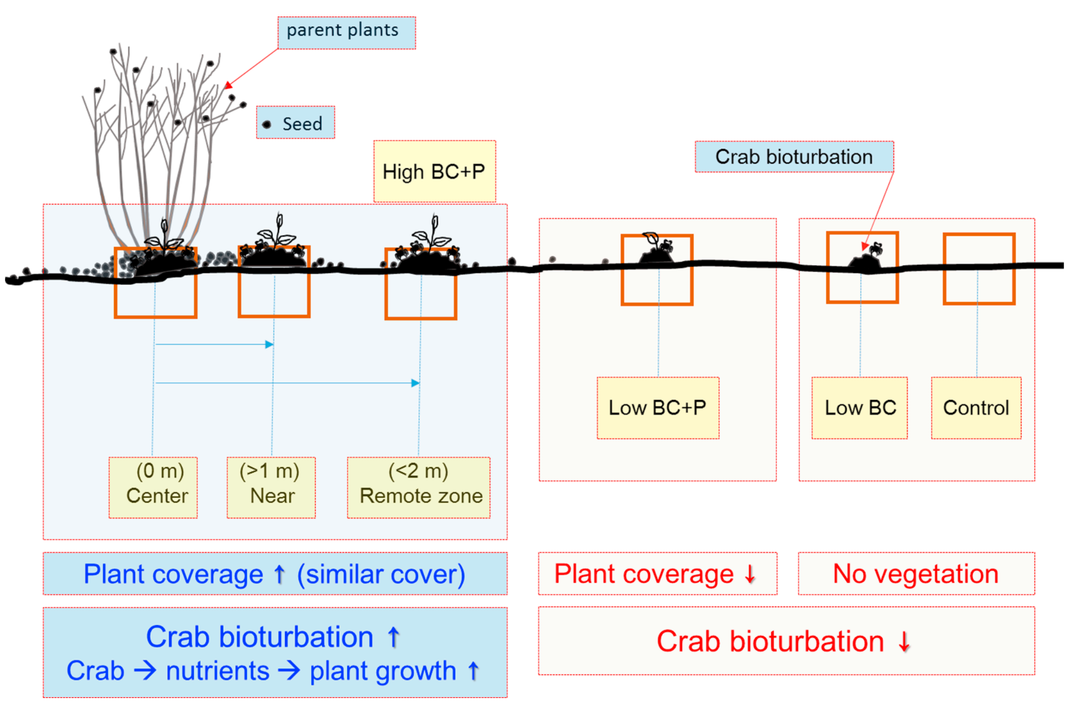

Fig. 5. A schematic diagram of effects of crab and halophyte on habitat types.

5. Conclusions

The growth of the halophytes was significantly affected by the density of the halophytes. The density of burrowing crabs can vary depending on the growth of the halophytes. Burrowing crabs may facilitate the growth of the halophytes. Also, the combination of burrowing crabs and halophytes significantly increased the spatial heterogeneity of soil physicochemical parameters in a salt marsh ecosystem. Therefore, burrowing crabs and halophytes can be important factors in salt marsh ecosystem processes and functions. Considering the high densities of burrowing crabs and halophytes often found in temperate salt marshes, it is necessary to pay more attention to their roles in this ecosystem.

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Appendix A. Supplementary data

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